ECOLOGICAL MONOGRAPHS

VOL. 21 OCTOBER, 1951 NO. 4

OFFICIAL PUBLICATION OF THE ECOLOGICAL SOCIETY OF AMERICA

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PUBLISHED QUARTERLY BY DUKE UNIVERSITY PRESS
DURHAM, N. C., U. S. A.

ECOLOGICAL MONOGRAPHS

A QUARTERLY JOURNAL
FOR ALL PHASES OF BIOLOGY

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Agents in Great Britain: The Cambridge University Press, Bentley House, 200 Euston Road, London, N.W. 1. Prices can be had on application.

Entered as second-class matter December 18, 1930, at the Post Office at Durham, North Carolina, under the Act of Congress of March 3, 1879.

AN ECOLOGICAL STUDY OF THE MID-APPALACHIAN SHALE BARRENS AND OF THE PLANTS ENDEMIC TO THEM

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INTRODUCTION

The term "barren" is frequently used botanically to designate an area more or less deficient in the type of vegetation normal for the region in which it is located. Thus the term "shale barren" has been aptly given to certain shale slopes of the mid-Appalachian region (Figs. 1-4) which support a sparse scrubby growth of oak, pine, juniper, and other woody plants and between which exists an open herbaceous cover dominated chiefly by several endemic or near-endemic species.

The purpose of this investigation has been to determine for these shale barrens (1) the physical nature of their environment, (2) response of the vegetation to this environment, and (3) the causes and nature of the endemism present.

I gladly acknowledge my indebtedness to a number of people for assistance in this investigation and regret that all cannot be mentioned here. Of those in the Department of Botany of the University of Pennsylvania, I am particularly grateful to Dr. Edgar T. Wherry for suggesting this problem and for his continued keen interest, judgment and advice, to Dr. J. R. Schramm and Dr. David R. Goddard for help especially with the physiological aspects, and to Dr. Ralph O. Erickson for aid liberally given in many

Fig. 1. Looking north in early spring towards a high ridge of Brallier shale along the Cowpasture River, Bath County, Virginia. Note the barrens formed on the crest of each flank of the ridge. The barrenness of bluffs in the foreground has been accentuated by stream action.

ways, but particularly with regard to problems on population studies. Dr. Erickson made the photographs for Figures 1, 2, 4, 14, and 18, and Joseph M. Devlin of the University of Pennsylvania kindly made the drawings for Figure 5.

The work was made possible in part by the following aid for which I am grateful; a Grant from the Research Committee of the Virginia Academy of Science, a Grant-in-aid from the the Research Committee of Emory University, and a Grant-in-aid from the National Society of Sigma Xi.

REVIEW OF LITERATURE

The classic shale barren slopes from which most of the earlier species descriptions and observations were made are on Kates Mountain near White Sulphur Springs, West Virginia and on hillsides along the Chesapeake and Ohio Railroad south of Millboro, Bath County, Virginia. While successively Michaux, Pursh, Rafinesque, Watson, Small, Britton, and MacKenzie (Wherry 1930) described species endemic or highly characteristic of these areas and probably traversed them many times, it was not until 1911 that they were specifically designated as unusual plant habitats, and given the name "shale barrens." At this time Steele (1911), in a paper describing five new species of plants found on the shale barrens, made these observations:

"Several of the species considered are inhabitants of a type of land widely distributed through the mountains of middle Virginia which might well be denominated "shale barrens." This land is made up of exposures of shale in different stages of disintegration, these at the point chiefly investigated consisting of the Romney formation of the lower Devonian. In the valleys these are reduced to a heavy clay, originally covered with good forest and when cleared susceptible to tillage. But the declivities and uplands bear at most a low and open growth of oak and pine, or frequently a still lower growth of scrub oak, kalmia, and other shrubs, in either case with an admixture of herbaceous plants. The formations are so open that over large areas they can be penetrated on foot with no great difficulty. The barrenness is perhaps largely due to the constant washing away of the finer particles of soil, but in some cases it seems as if it must be chargeable to chemical composition. The plant covering, I should say, is mildly xerophytic, but there is no evidence of extreme drought. On the contrary, the vegetation maintains itself through the season, even on sunbeaten slopes as well as that on other soils similarly situated. The variety of plant life is very considerable, and together with many plants well known on other strata, these barrens possess a number of species peculiar to themselves."

Wherry (1925, 1929, 1930, 1933) published a series of papers which were chiefly concerned with the taxonomic and geographic aspects of the endemic flora. His third paper included the geographical distribution of the barrens, an annotated list of the more notable species, a chronological list of the endemics and near endemics, and observations on the ecology of these areas. In these observations Wherry agrees essentially with Steele but goes further in stating that:

"These barrens are developed on shale slopes—places where hard shaley rocks of the Romney (Middle Devonian) and Jennings (early Upper Devonian) formations outcrop on steep hillsides, the surface being strewn with frost-broken fragments. They are typically occupied by a . . . sparse plant growth . . . grading into normal woodland wherever conditions permit the accumulation of sufficient soil. . . . The peculiarities of the shale-slopes which lead to their being occupied by endemic plants appear to be the sparsity of soil, the way in which the loose rock-flakes creep down the slopes under the influence of the weather, and the limited amount of available moisture and nutrient elements. The rock is made up largely of quartz and clay minerals, and exhibits a neutral reaction. The accumulation of humus in the heaps of loose fragments results in the development of considerable acidity, little mineral matter capable of neutralizing the organic acids formed being present. The litter is evidently too porous to permit the accumulation of much available nitrogen, and tests have failed to show the presence of nitrates or ammonia in appreciable amount."

Later, in the same paper, Wherry ascribes the limitation of the barrens to the mid-Appalachian mountains to "changes in physical and chemical character exhibited by these Devonian strata along their strike."

Core (1940) essentially agrees with Steele and Wherry in the preface to a paper containing a list of the shale barren areas in West Virginia and an annotated list of the species found on them.

Although no other work has been published on a broad geographic scale for these areas, two papers have appeared which dealt with the shale barrens of the Massanutten Mountains in the Shenandoah Valley of Virginia. Artz (1937) gives a list of the plants found on the barrens and associated shale slopes, and includes a brief discussion of four endemic plants with special reference to their root systems. Allard and Leonard (1946) made an intensive, chiefly floristic, study of the Massanutten shale barren associations. Perhaps the best summary of their ecological explanations is as follows:

"It would appear that the lack of a true soil, its instability, exposure to drying winds and sun, and the scarcity of available moisture and humus on the slopes are the limiting conditions restricting the plant life of these areas. . . ."

They furthermore conclude that successional stages are lacking both in the history and the probable future of the barrens, and that "the present vegetation is at once the climax itself."

These investigations have dealt primarily with the taxonomic and floristic aspects of the shale barrens and were not intended to deal with the ecological aspects much beyond the observational level. Because of this and the unique character of the barrens it is quite understandable that the ecological interpretations given in these papers are not in complete agreement either with each other, or with the findings presented in this paper. Rather than solve, they emphasize the many complex ecological problems of these barrens, and clearly indicate the need for an experimental approach to their solution.

METHODS

This investigation is based upon experimental studies carried on in the field and in the laboratory. Field work was inaugurated the middle of September, 1946. Fourteen days were spent then in an exploratory study of the shale barrens of Alleghany, Bath, Botetourt, and Craig Counties, Virginia, with emphasis on a familiarization with characteristics of these areas, and discovery of new stations for plants endemic to them. In early May, 1947 four days were similarly spent exporing the shale barren region of south-central Pennsylvania and Maryland. In mid-June a five-day trip was made for the same purpose through the shale barren areas of West Virginia. For 12 weeks, from late June to mid-September, 1947, with headquarters at the University of Virginia Biological Station in Giles County, Virginia, one to three-day trips were made almost every week into the shale barren region, with emphasis placed on collection of precise ecological data. Two three-day field trips were made through the southern part of the region in the spring of 1948, one around the first of April and another three weeks later, for the purpose of studying barrens at the time spring growth was just beginning. Finally in mid-June a ten-day trip was made throughout the whole area, with the specific purpose of rechecking in the field conclusions drawn in the course of the investigation.

FIG. 2. A shale barren in early spring 5 miles n.n.e. of Clifton Forge, Alleghany County, Virginia.

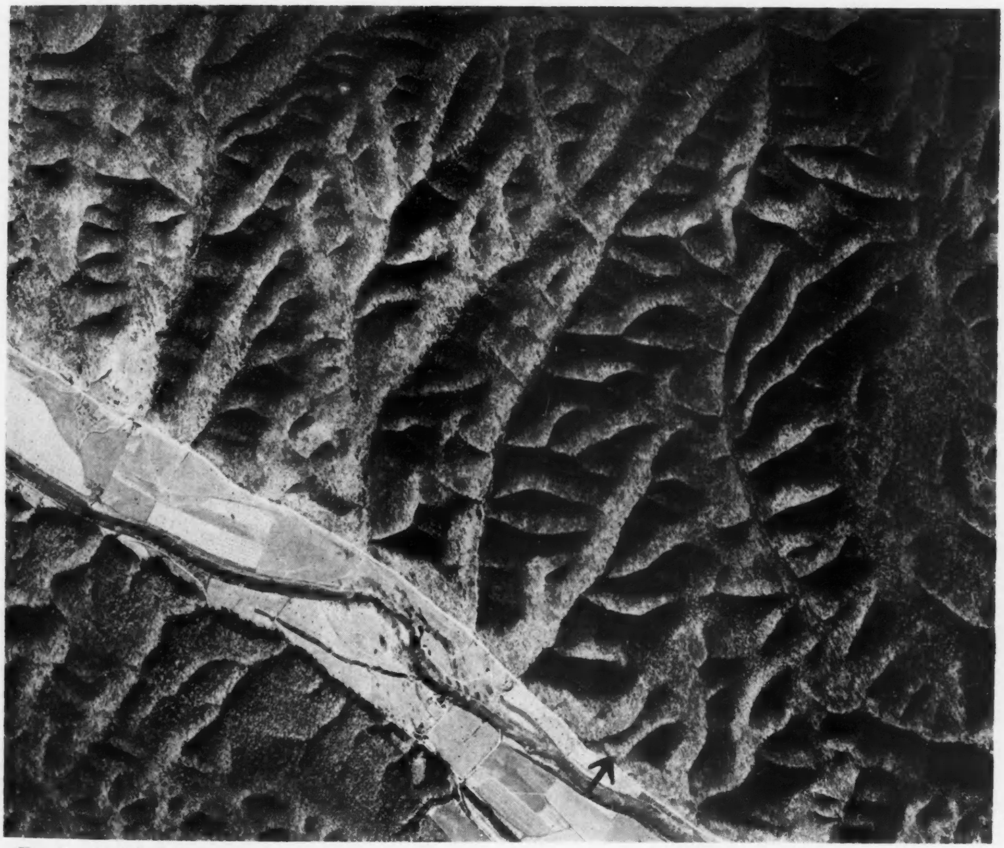

FIG. 3. Aerial photograph of terrain near Eagle Rock, Botetourt County, Virginia. All of the area north of the agricultural strip is Brallier shale. Note the barrens which occur on each south facing slope of this formation, as indicated by the sparse vegetation. The crowns of large trees are highlighted on the north slopes. The arrow indicates the experimental area shown in fig. 4. Scale ca. 3 inches per mile. Photograph BV2-03, Nov. 17, 1936 by U. S. Forest Service.)

FIG. 4. Looking north in early spring towards the low ridge of Brallier shale near Eagle Rock, Botetourt County, Virginia, on which the experimental area is located. Station 2 is within the white circle and Station 4 is below the black arrow.

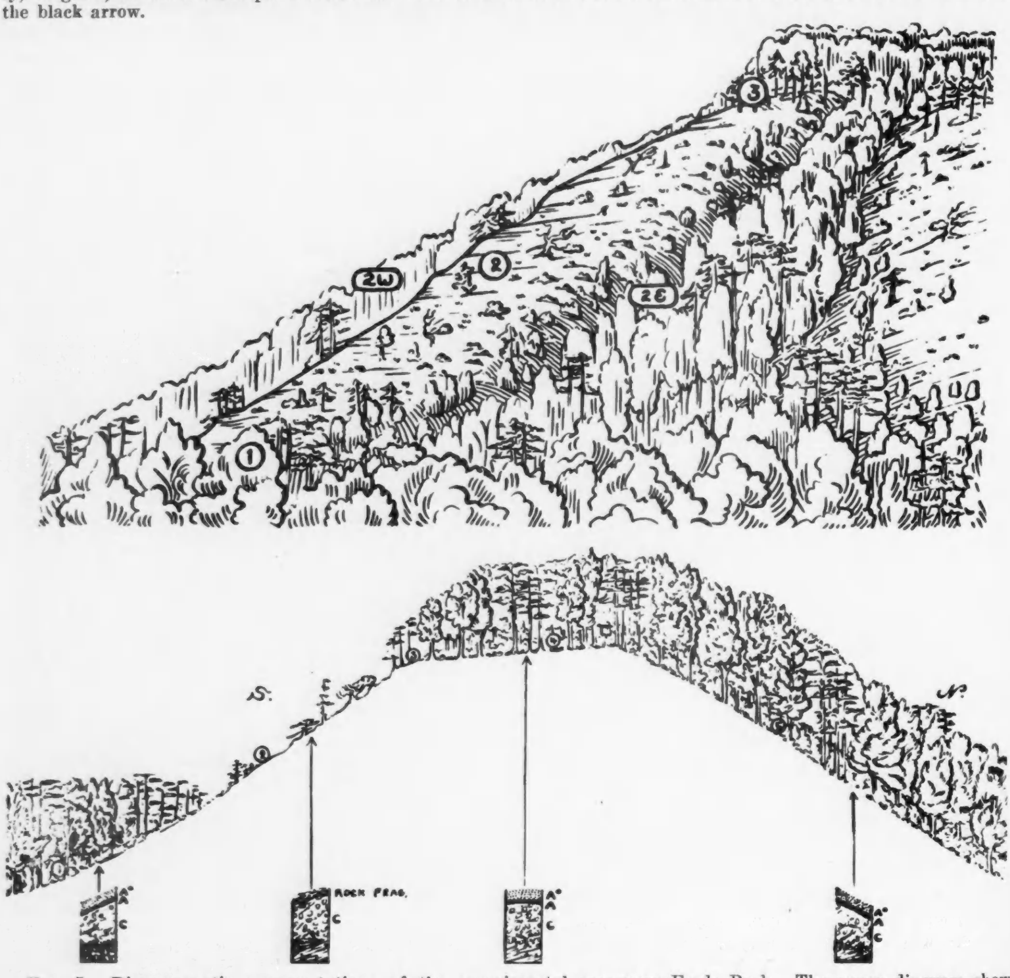

FIG. 5. Diagrammatic representations of the experimental area near Eagle Rock. The upper diagram shows locations for Stations 1, 2W, 2, 2E, and 3. The lower one shows locations for Stations 1, 2, 3, 4, and 5, and also indicates typical soil profiles for four of them.

In these field studies, it was soon evident, as it had been to other students, that the barrens are essentially alike throughout their whole range. It was therefore advisable to study intensively a particular barren, rather than to make a more superficial study of representative barrens distributed over the whole area. In June 1947, a typical barren herein designated as the "experimental barren" was chosen near Craig Creek, 2.5 miles northwest of Eagle Rock, Botetourt County, Virginia. This barren was selected because it was easily accessible, hidden from the curious eyes of the local residents, and received a minimum of road dust. The vegetation on it and on all adjacent areas was relatively free of the effects of fire and of man. Its slope does not exceed thirty degrees, and has not been accentuated by stream action in recent geological time.

The barren selected (Figs. 3-5) is one of many occurring on a series of hills of 200 to 400 feet relief, and occupies the crest of a small south-facing ridge which flanks one of the hills. The barren extends for about 75 yards along the narrowly rounded middle portion of this ridge, and for about 20 yards on either side. At its base is a talus slope with well developed soil. The base of this talus slope is cut off by an unpaved county road and an old shale quarry, while beyond it is a quarter-mile wide strip of cultivated alluvial soil, ending at Craigs Creek. On both sides of this ridge are small dry ravines, with dense tree cover and good soil, but a sparse shrub and herb layer. At its upper end the ridge rounds off gradually to a fairly level top, some 60 yards across, while to the north it slopes downward at approximately the same angle as that for the barren side. These areas adjacent to the barren are covered with chestnut oak, hickory, pine woodlands characteristic of this region. Although the barren passes gradually into woodland on either side and at the base, the change on its upper side is decidedly abrupt.

To learn the peculiarities of factors characteristic of barrens and how they differ from adjacent areas, seven stations were established for their study (Fig. 5). Station 1 was located on the talus slope, Station 2 on the most exposed part of the barren at its lower end, Station 2W and Station 2E in the ravines to the west and east respectively, Station 3 in the transition zone at the upper end of the barren, Station 4 in the center of the flat woods at the top, and Station 5 fifty yards down on the north slope. Wherever indicated by the course of the problem, data obtained on this barren were supplemented by and checked against similar data obtained from other barrens.

Experiments, designed to correlate and supplement those in the field, were conducted in the laboratories of the Department of Botany of the University of Pennsylvania. Growth experiments, unless otherwise indicated, were made with soil transported from the experimental barren and from nearby ones.

Soil and plant temperatures were obtained by use of a resistance thermometer, known as a thermistor, according to the technique of Platt and Wolf (1950). The 0.02 mm. diameter sensing element and its high sensitivity of 0.01 degree C made it possible to obtain reliable measurements within small spacial limits.

Temperature tolerances were determined by the method described by Platt and Wolf (1951). By this method the subjects are placed on a klinostat, and radiant energy supplied by infra-red lamps placed over them. Energy intensity is controlled by use of a variac and by adjusting height of lamps. The resulting controlled temperature gradients are similar to soil gradients and approximate air gradients obtained under natural conditions of insolation.

Techniques of limited application are described elsewhere in the paper.

THE ENVIRONMENT

Geology and Lithology

Factors primarily responsible for the origin and continuation of the shale barrens are based on the unusual lithological character of a single shale formation of the Upper Devonian, the Brallier. Especially because of the key role played by this one stratum, and also because of certain misunderstandings which have arisen in the past concerning the relationship of this stratum to the shale barrens, a full geological discussion follows.

The shale barrens (Fig. 6), usually referred to the mid-Appalachian Mountains, are located more precisely in that part of the Appalachian Valley or Valley and Ridge Province of the Appalachian Highlands, extending from south central Pennsylvania through Maryland and eastern West Virginia to southwest Virginia. The Appalachian Valley is naturally divided longitudinally into two belts. The southeastern belt, dominated by broad valleys with relatively few ridges, is commonly known as the Great Appalachian Valley. Here the shale barrens occur only on Massanutten Mountain, a prominent ridge extending for forty-five miles from Strasburg southwest to Harrisonburg, Virginia, and on certain ridges in Roanoke and Montgomery Counties, Virginia. On Massanutten Mountain there are also some partially developed barrens on shale of different geologic age, namely Martinsburg of the Upper Ordovician, as discussed below. In the northwestern belt, dominated by high, narrow, linear northeast trending ridges with interspersed narrow valleys, are found the majority of the barren areas. Here they occur primarily on small hills along the valley floors and on lower flanks of the ridges. Although the maximum elevation in the whole region is 4224 feet, the barrens are, with few exceptions, at elevations of 1000 to 2000 feet above sea level.

Sediments of this province, laid down during the Paleozoic within a narrow geo-syncline extending from Newfoundland to Alabama, resulted at the close of this era in a great lens-shaped stratified layer of

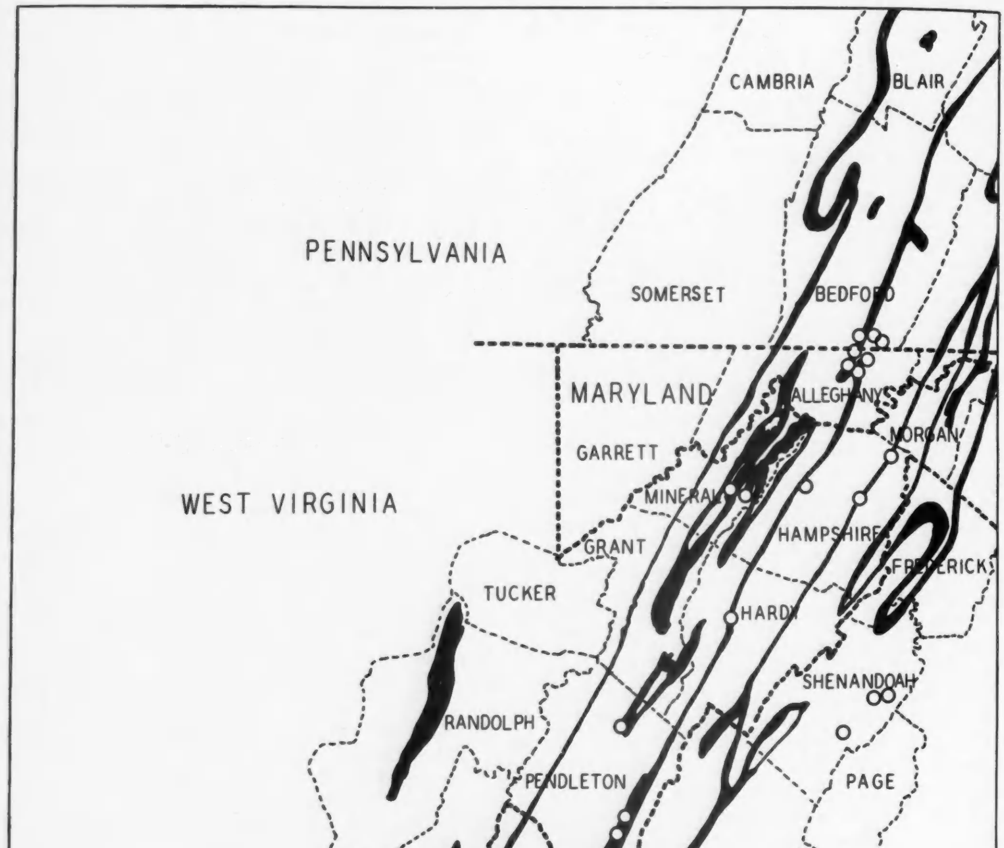

FIG. 6. Map of shale barren region, showing outcrops of Brallier shale. Dots represent known shale barrens, or groups of shale barrens.

shales, sandstones, conglomerates, and limestones, totalling a maximum thickness of 8 to 10 miles. Within the past 185,000,000 years this area has been laterally buckled and crumpled into its present inclined attitudes, and at intervals vertical uplift has maintained its elevated position in spite of great wastage by erosion. The area has been completely peneplained at least once, and partially peneplained several times. During these processes the hard sandstones have formed the ridges, while the valleys have been carved from the softer shales. Thus the long narrow exposures of the shale, as shown on the map, were formed. The shale barren area is drained to the east by tributaries of the Potomac, James, and Roanoke Rivers and to the west by those of the New River.

A detailed discussion of the stratigraphy, structure, and history of these formations may be found in Butts' (1940) geological treatise on the Appalachian Valley of Virginia, and in part, in Woodward's (1943) treatment of the Devonian system of West Virginia.

Terminology used for the various Devonian strata is confusing in that there is variation in respect both to the geological publications of the four states concerned and to the times at which these were published. For example the referring of the barrens to the Romney by Steele (1911), to the Romney and Jennings by Wherry (1930) and to the Brallier in this paper are all consistent with the geological literature. This is shown in Table 1 which gives the comparative terminology of the middle and upper Devonian formations.

This table is based on terminology used in the latest State Geological Maps of Pennsylvania (1931), Maryland (1933), West Virginia (1932), and of the Appalachian Valley in Virginia (1933). According to Butts (1940) the original usage of the term Romney, as described by Darton in 1892, included all the strata extending from the Oriskany sandstone to his

TABLE 1. Comparative terminology of the middle and upper Devonian formations occurring within the mid-Appalachian Mountains. (Compiled from latest State Geological Maps.)

	This Paper	Virginia	West Virginia	Maryland	Pennsylvania
Upper Devonian	Catskill	Catskill	Catskill	Hampshire Catskill	Catskill
	Chemung	Chemung	Chemung	Jennings	Chemung
	Brallier	Brallier	Portage		Portage Genessee
	Genessee	(Not present)	Genessee		
Middle Devonian	Hamilton	Romney	Hamilton Marcellus and Onondaga	Romney	Hamilton Marcellus and Onondaga
	Marcellus				
	Onondaga	Onondaga			
	Oriskany	Oriskany	Oriskany	Oriskany	Oriskany

own Jennings formation. Subsequent to Steele's publication, Butts in 1918 recognized the lower half of the Jennings as the Brallier, while earlier, Stose and Swartz in 1912 had removed a black shale, the Genessee, from the upper part of the Romney and included it as the lowest division of the Jennings. Still later the Onondaga shale and limestone was removed by Butts from the Romney, leaving the Romney restricted to include only the Marcellus and Hamilton members. Other misunderstandings, as in part by Core (1940), are due either to the difficulty in accurately plotting shale barren locations on these narrow bands of shale, often but two or three miles in width, from data supplied by the earlier collectors, or failure to distinguish between true and temporary barrens. Frequently through the interference of man, slopes on Romney shale become quite barren, are slow to revegetate, and thus may come to be occupied by some of the characteristic shale barren species of plants. However, these temporary barrens lack other characteristics, and with experience can be differentiated.

Since the shale barrens are obligate upon certain lithological characters possessed chiefly by the Brallier, and only within small areas by other shales, only this formation has been plotted in Figure 6. Dots on the map represent specific locations which have been explored on foot, and on which endemic species have been collected. These are only a small fraction of the hundreds of shale barrens occurring on this formation within the shale barren region. The location of each dot was checked in the field and plotted directly on to the corresponding geological and topographical sheets.

A comparative study of the characteristics possessed by the middle and upper Devonian strata (Butts 1940; Woodward 1943) clearly shows that the Brallier, in contrast to the others, is a unique formation. Woodward says that "With a lithologic constancy that is both remarkable and matched by few other formations, the Brallier shale maintains the same appearance and character throughout its entire surface extension from central Pennsylvania nearly to southwest Virginia." Whereas, in its range here referred to, it is more fissile, siliceous, and weather-resistant than the other shales, in southwest Virginia it becomes more clayey and carboniferous and weathers readily into round hills and flat valleys (Fig. 7).

Thus two characteristics of the Brallier shale stand out. One is its resistance to weathering, and the other its lithologic constancy throughout most of its range. The former characteristic is responsible for the numerous natural rock outcrops of this formation, as well as for the mantle of thin rock flakes which cover the soil on the shale barrens, and which are significant in maintaining in a stable condition their barren nature. The second characteristic explains the geographical limits of these barrens on the Brallier. Southwest of the area on the map

FIG. 7. Undisturbed surface of Station 2 of the experimental area near Eagle Rock, reduced one-half. The weather resistance of the shale is indicated by the sharp edges of the rock fragments.

at which the known barrens terminate, the shale changes in its nature to one more clayey and carboniferous, resulting in rounded hills and flat river valleys with few natural exposures. Wherry particularly, as well as the writer, has crossed and traveled along these exposures in an attempt to extend the barrens in this direction. However, there was not even an indication in the topography or in the vegetation that they occur here. Increased rainfall is undoubtedly a concomitant factor. Northeastward the barrens extend sporadically through Bedford and Fulton Counties of Pennsylvania, but disappear farther north, where the shale, as well as diminishing in its exposure, again becomes softer and more easily weathered.

Despite this constancy in character, variations do occur in the Brallier within the shale barren area, and are primarily responsible for the discontinuities in the shale barren distribution shown on the map in Figure 6. Although it is often difficult to separate lithological effects from those of rainfall and slope, there are places, even within the same range of hills, where such variations are difficult to explain on any other basis. Such is the case in the range of hills between Hot Springs and Bacova Junction in Bath County, Virginia, where but one or two out of a dozen similarly situated hillsides have a normal vegetation, or in a range of hills along the road northeast of Deerfield, Augusta County, Virginia, where the reverse is true. These variations are even more evident between adjacent large exposures of shale as occur in the southeastern corner of Pendleton County, West Virginia. Within a few miles radius of Brandywine, the hills are prominently barren, but southward for a distance of fifteen miles along the same outcrop and extending into Virginia, bluffs are rare along the streams and the hills are less barren, infrequently producing typical barrens. Woodward (1943) notes that the strip of Brallier for a length of 25 miles south of Moorefield (Hardy County) is more wooded and softer than that of the same strip in its northward extension. The most notable change is found in the relatively broad outcrop of Brallier shale at Elkins, Randolph County, West Virginia. This was examined with some care, for no shale barrens had been reported from there. Although many excellent exposures of the Brallier are afforded by road cuts and the like, natural bluffs and steep hillsides are quite uncommon, and the area resembles in its topography and vegetation the non-barren areas in southwestern Virginia. The rainfall here, as in southwest Virginia, is several inches higher, and doubtless exerts some influence upon the vegetation.

The strike of the shale strata appears to have little influence in the formation of barrens, for they occur on every configuration of the strata. These configurations, however, affect the intensity of the barrenness through their effect upon runoff and retention of rain.

The only known exceptions to this relationship of the Brallier shale to barren formation are found on the Massanutten Mountain in the Shenandoah Valley, on the southwestern end of Fort Lewis Mountain in Roanoke County, Virginia, and in Mineral County, West Virginia. In every case examined, however, the substratum possesses much the same lithological characteristics as those of the Brallier.

On Massanutten Mountain, where the Hamilton member of the Romney outcrops in the center of the Massanutten syncline along Passage Creek, typical shale barrens occur especially at one and two miles south of Elizabeth Furnace. Butts (1940) notes that the Hamilton here is a compact, very fine-grained, olive green, argilliceous sandstone with a hacky fracture.

Also on Massanutten Mountain the Martinsburg shale of the Upper Ordovician, a stratum usually weathering easily and forming deep soils, changes in its nature where shale barrens are formed to one similar to that of the Brallier. Allard and Leonard (1946) believe that the barrens here are caused by the capping of the softer Martinsburg shales by a hard resistant sandstone, thus producing slopes on which erosion is greatly accelerated. Observations made in the course of this investigation can scarcely support this explanation. Certainly the overlying sandstone is responsible, at least in part, for these slopes, but barrens occur on those having only a 20 to 40 degree pitch, and there are many similarly situated slopes on this same shale in this area which are fully vegetated. The particular Martinsburg stratum on which shale barrens occur is soft only in respect to the capping sandstone, but is much harder than that of its other extensive outcrops on this mountain. The lack of erosional gullies, the litter of resistant rock fragments which covers the ground, and the absence of a normal ground cover, along with other peculiarities, as interpreted by the data in this paper, provides ample support for this stand. The photographs published by Allard and Leonard of

slopes similar to those observed in this study strongly indicate the same conclusion. This same shale becomes even harder along the west side of the mountain, south of Strasburg, where the North Fork of the Shenandoah River has cut deeply into its sides. Butts (1940) says that the basal parts of these beds are composed of a black slaty calcareous shale, and an excellent example may be seen of this on the barrens situated above the hydo-electric dam 2 miles west of Edinburg.

While the writer has not examined the barren on Fort Lewis Mountain, again situated on Martinsburg shale, the observations (personal communication) of Dr. Carroll E. Wood, Jr. who discovered this area, as well as a study of the topography sheets, suggests the same explanation as that given for the Massanutten barrens.

Core (1940) in his map showing the distribution of shale barrens in West Virginia plotted only the Romney formation, and in the text refers certain barrens specifically to this formation. Most of these were observed and in each case, when plotted, fell within the Brallier. Core, by correspondence kindly explained this seeming contradiction. He states that in visiting these barrens he did not attempt to identify the formations, and that his use of the term Romney according to the staff of the West Virginia Geological Survey, was based on an old usage in which it designated a more inclusive series of rocks, including the present Brallier.

TOPOGRAPHY

All available evidence indicates that topography plays a specific role in shale barren formation. Slope angles were determined by estimate and by means of an improvised inclinometer, consisting of a rectangular board marked from one corner into 15 degree segments. On slopes of less than 20 degrees, forces controlling the balance between degradation and accumulation of surface soil and leaf litter permit development of a normal vegetation. However, as the pitch increases, this balance must shift for the slopes pass gradually or suddenly into a barren condition. On the whole, barrenness becomes more pronounced as slope increases. This relationship may lead to the false impression that the barren formation is restricted to certain bluffs and steep hillsides which have been formed by undercutting of shale strata by stream action. Such an impression is heightened in that barrens are usually seen from roads, which in this region mostly parallel streams. Stream action is apparently influential only through its effect on slope, as indicated by (1) lack of barren formation under such conditions in softer shales of the region, (2) occurence of a greater number of barrens away from streams than along their course (Fig. 3), and (3) frequent occurrence of barrens on the flanks of ridges well above the valley floors. Notable examples of the latter occur on Kates Mountain south of White Sulphur Springs, and along the high ridge west of the Cowpasture River extending from 6 to 15 miles northeast of Clifton Forge, Virginia (Fig. 1).

Topography may be used as one of several lines of evidence which demonstrate that shale barrens are not the subject of extreme erosion. If a differential rate of erosion occurred over the thousands of years at least that the shale barrens have been in existence, then a difference would have developed between the angle of slope for the north and south sides of these hills. While means were not available to accurately measure small differences that may exist between these slopes, an evaluation was possible of substantial differences that might occur: i.e., examination of topographic sheets and aerial photographs, observations made from a distance on north-south profiles as well as those made on the slopes, evidence obtained from a study of soils, surface characters, and surrounding vegetation, and data from two types of experimentation described later. All failed to indicate any cause for, or presence of, consistent or significant differences between the slopes of continous north-south profiles.

EXPOSURE

The factor of exposure, like lithology and topography, is apparently critical and absolute in the formation of shale barrens. On moderately steep slopes barrens have been found only on those areas having a southerly exposure. Development on east and west exposures have been observed only where stream action has produced very steep slopes and bluffs whose steepness compensates in part for the reduced period of insolation. Although northerly facing bluffs may be deficient in vegetation, that present has little relationship to the vegetation of slopes receiving sunlight for most of the day. Observations would indicate that when north facing bluffs are reduced by forces of erosion, succession normal to that of any north facing slope occurs and barrens are never formed. The relationship to exposure is particularly striking along a ridge or row of hills where each southerly exposed slope alternates in its barrenness with the normal woodlands of the less isolated and moister adjacent ravines and hillsides (Figs. 1 & 2).

CLIMATE

The climate of the shale barren region from south-central Pennsylvania to southwest Virginia is fairly uniform in all respects. Although this area extends through almost 3 degrees of latitude, from 37° 15′ to 40°, the influence of the long narrow northeast-southwest trending ridges and valleys is such as to cause the isopleths of the various meteorological factors to take the same directional trend. This is demonstrated in the general climatic maps of the United States and in the more detailed climatic maps of individual states presented in the U. S. D. A. Year Book, *Climate and Man* (1941), as well as by the rainfall isopleths given in Figure 8.

For these reasons, that part of the Appalachian

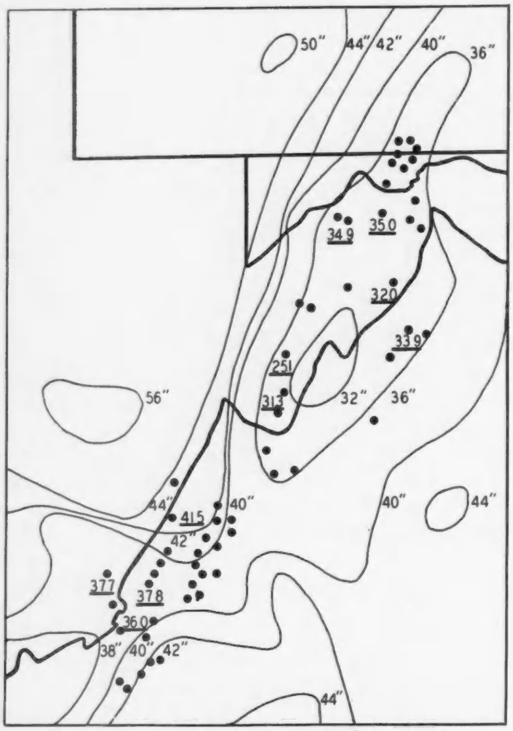

FIG. 8. Average annual precipitation of the shale barren region, extracted from the Section on *Climates of the States*, U.S.D.A. Yearbook, *Climate and Man*, 1941. Figures underlined are mean annual rainfall for weather stations located near shale barrens. Dots represent known shale barrens or groups of shale barrens.

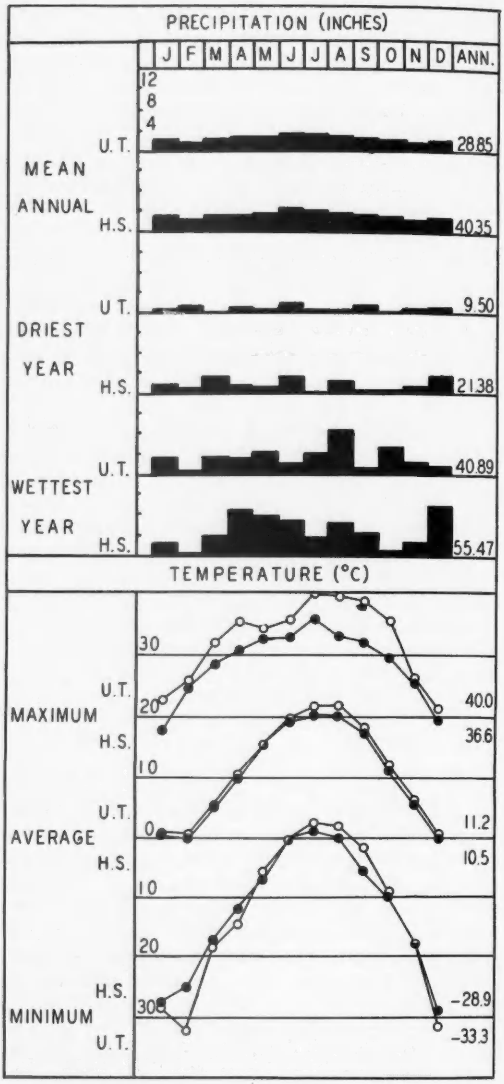

FIG. 9. Representative precipation and temperature averages and extremes for shale barren localities. Upper Tract (U.T.), Pendleton County, W. Va., has the lowest, and Hot Springs (H.S.), Bath County, Va. one of the highest precipitation rates recorded for this region. The graphs are based on records continuous from 1898 to 1930 for Upper Tract, and from 1892 to 1930 for Hot Springs. The driest year for both was 1930, while the wettest year for the former was 1898 and for the latter 1901. (Data from *Climatic Summary of the United States*, Section 91 and 93, U. S. Weather Bureau.)

Mountains which contains the shale barrens lies in a southern tongue-like extension of the climatic zone common to the northeastern United States. Köppen and Geiger (1936) characterize this as a warm, temperate, rainy climate, with no distinct dry season. In such a climate the average temperature of the coldest month is below 18° C, but above -3° C; the average temperature of the warmest month is over 10° C, and the driest month of summer receives more than 1.2 in. of rain. Köppen and Geiger's classification for this region agrees essentially with that of Thornthwaite (1931), in which he used the unique criteria of precipitation effectiveness and temperature efficiency.

The general meteorological data given for this region are subject to cautious interpretation on two counts, with respect to the individual shale barrens. One is that because of the rugged topography, certain factors vary widely within small geographic limits, while the other is that but few First Order Weather Bureau Stations are maintained here, and information is far from complete.

An indication of the monthly and annual ranges and extremes of rainfall and temperature for this region is given in Figure 9.

SOILS

From a distance, the most distinctive character of a barren is its expanse of brownish yellow soil, interrupted only by profiles of scattered trees, shrubs and herbs and on the steeper slopes by vertical exposures of more resistant interbedded strata. On

closer examination, this soil is seen to be covered by a thin mantle of flattish and variously sized weather resistant rock fragments, washed clean by the rain, and so easily displaced as to form small avalanches of rock when trod upon. One immediately has a convincing impression that here is a skeletal soil, severely leached and thus low in nutrients; easily displaced by forces of heat and cold, rain, snow, hail, and frost; and subject to desert-like temperature and moisture conditions. It is quite logical then, that various combinations of these observations are the ones that have been used to explain the sparsity of vegetation on the barrens. That these previous explanations are essentially incorrect is demonstrated in this paper. However, it is improbable that the ecology of the shale barrens could have been realized without employment of precise experimental methods, in respect both to environmental factors and to their vegetational response.

SOIL FORMATION

The Brallier formation is composed of stiff, thinly laminated, micaceous, and highly siliceous shale thinly interbedded with sandstone of similar characteristics. Both weather to a thin debris. The green, olive green, or gray green colors of the parent rock quickly weather to yellows and browns.

Examination of the soils derived from this substratum indicate they most closely correspond to melanized or humus-incorporated soils, often called "black top" soils (Wilde 1946). In such soils there is little translocation of either sequioxides or of silica, and consequently nearly all of the constituents are fixed *in situ*. Humus is gradually incorporated into the parent material from the surface downward, as is shown by the percentages of humus given for different soil depths in Figure 10, with the result that the A, B, and C horizons are not clearly differentiated. Especially the characteristic B horizon or eluviated zone, as is developed in mature podzolic and lateritic soils, is lacking. These facts necessitate for convenience an arbitrary division of the soil profile into A and C horizons, as is used here.

Whereas most humus-incorporated soils are several feet in depth, those derived from the Brallier are relatively shallow. About 150 measurements have been made with spade and soil auger. From these measurements and from observations of highway and railroad cuts, the depth varies from 4-12 inches, the average depth being 8-10 inches. A typical development of Brallier soil, derived under optimum conditions, is that occurring at Station 5 on the north slope of the experimental area near Eagle Rock. The A_0 horizon is composed of 4 to 6 inches of duff, whose upper layer of raw leaf litter gradually passes into a bottom layer of moist partially decomposed humus, often penetrated by numerous small roots. Below this about one inch of fine black humus incorporated with mineral matter constitutes the so-called A horizon. From this, the organic content thins imperceptibly through 6 to 10 inches of weath-

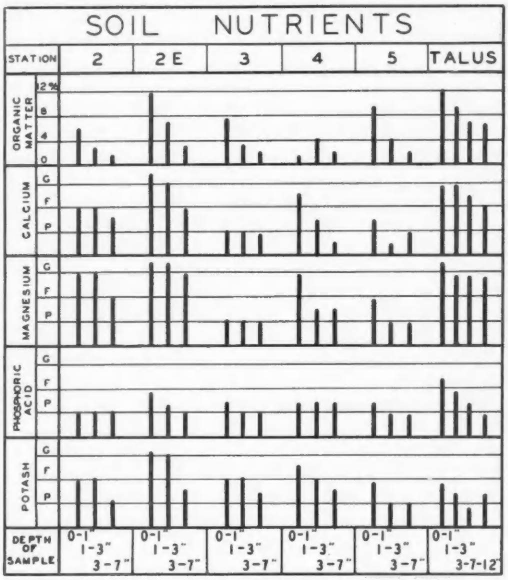

FIG. 10. Soil nutrient determinations by rapid colorimetric methods for the experimental area near Eagle Rock. G indicates good, F indicates fair, and P indicates poor.

ered parent material to the bedrock, forming what is here called the C horizon. The C horizon, gray above due to the higher organic content, blends downward into a deep yellow fine silt loam, and contains throughout from 20-50% of variously sized unweathered fragments of the parent material. At its base the unweathered bed rock, while solid enough to stop a shovel or soil auger, is loosely fragmented and embedded in the same silt loam for a depth of one to several feet. Soils formed in drier habitats, as on the wooded ridge top at Station 4, differ in that the leaf litter is less decomposed and the A horizon more sharply delimited and usually thinner.

The only significant difference obtained in this investigation between the soil profile of a typical shale barren and that of a normally vegetated slope is the substitution of a thin mantle of rock fragments for the A_0 and A horizons.

This rock mantle however, attributable to the Brallier substratum, is in turn basically responsible for the sparsity of plant life on the barrens. The origin and continuation of this mantle may be briefly postuated as follows. In geological time, through normal processes of differential erosion and consequent dissection, the topography of this region has been formed. On less insolated and therefore well vegetated slopes of Brallier shale, the fragments of the substratum, though persisting for a while in the C horizon, ultimately weather to soil. On the more highly insolated slopes however, conditions favor persistence of rock fragments in the C horizon for a longer period of time. This slight difference per-

mits these unweathered fragments to accumulate gradually at the surface, as the weathered substrate of the C horizon in which they are embedded is gradually removed. This surface layer of fragments catches and holds an amount of organic debris adequate for an incorporation of humus in the C horizon equal to that found in the C horizon of vegetated slopes. Of course, an equilibrium is established for any given set of conditions. The established equilibrium on the barrens is such that the depth of the C horizon, as well as its moisture and nutrient content, is essentially similar to that of vegetated slopes.

The stability of this surface mantle of rock fragments is quite remarkable, particularly since it is easily dislodged into cascading rock streams when walked upon. This easy displacement by man or large animals is made possible by the rather abrupt contact existing between the rock fragments and the silt loam beneath. Its normal stability is strikingly demonstrated by the presence of a good growth of crustose lichens on many of the fragments, as well as by the conspicuous lack of accumulation or piling up of these fragments at the at the bases of the barrens; bluffs and very steep hillsides excepted.

However, since it has been suggested that possible shifting of these rock flakes was a unique characteristic of the barrens (Wherry 1930), additional evidence was desirable. This was obtained by tagging or marking the fragments, so that any change in position over a period of time could be detected. White lead paint, thinned 20%, was sprayed on the surface by means of an insect spray gun in stripes 6 to 12 feet in length and 6 inches wide, along the contour lines. Care was taken to avoid applying enough to cause a cementing of adjacent particles. Three stripes were painted on the barren near Eagle Rock on slopes of 20° to 35° pitch, and one on a barren near Millboro in Bath County, Virginia, with a pitch of more than 60°. The applications at Eagle Rock were observed weekly for five weeks, during which time 3 inches of rain fell, as measured by a rain gauge set up on the barren. At the end of this time, all three stripes were estimated to be at least 95% intact. Unfortunately, interference by man invalidated observations made the following spring. The stripe applied at Millboro was observed during and immediately after a violent rainstorm which arose only a few minutes after the stripe was applied. Except for small washes which removed three sections, each about 2 inches across, the stripe was almost intact. Other areas which had been marked by dyes applied to the surface remained without essential change for the 10 months' period observed.

pH AND SOIL NUTRIENTS

Hydrogen-ion relationships of soils derived from the Brallier are relatively uniform. Some 50 pH determinations show the barrens to have a pH range of 4.5 to 5.5, and those of the north slope to be somewhat more acid, with a range of 4.0 to 5.0. The deeper soil portions, more recently derived from the parent rock, are more acid that the upper ones which are older and have a higher organic content. Greater variability in hydrogen-ion concentrations occurs on the barrens of the Martinsburg Shales of Massanutten Mountain, where the substratum is more alkaline (Allard & Leonard 1946), but even there, on the barrens proper, the hydrogen-ion content of the upper layers of the soils is the same as those overlying the Brallier.

Three sets[1] of nutrient analyses were obtained. For direct comparison, samples for each set were collected at uniform depths in the soil. On vegetated slopes the A_0 horizon was removed and depth measurements made from the surface of the A horizon, while on the barren slopes measurements were from the surface of the rock fragment mantle, which there replaces the A horizon.

The first set (Fig. 10), collected in September, 1947 on the experimental area near Eagle Rock, was determined by rapid colorimetric methods. The second set, composited from eight series of soil samples collected for moisture determinations on the same area and at the same depths through the summer of 1947, were similarly determined. Since these determinations essentially parallel those of the first set, they are not presented in detail. For the third set, collected on and near the same area in September, 1947, determinations were obtained by precise analytical methods, as shown in Table 2. These agree essentially with the other two sets.

Because of the low economic value of the upper Devonian shales, few gross chemical analyses have been made of them; and none have been found for the specific substratum underlying a barren area.

These determinations indicate a surprising similarity for horizons sampled between north and south slopes. The top 3 inches of barren soil, including the layer of rock fragments and the upper portion of silt loam, is in some instances even richer than the top 3 inches of the north slope, which includes the A_0 horizon. C horizons, sampled from the 3-7 inch depth, are likewise about equal upon the two slopes. Extensive field observations of color, structure, and texture of Brallier soils, when combined with other findings in this paper, strongly suggest that this relationship holds true for all barren areas.

Two significant items not included in these data are (1) the A_0 horizon of the north slope, composed of 4-6 inches of duff and leaf mold, and (2) the moisture content of the upper 3 inches of soil sampled. The excessive dryness of the barren surface throughout most of the growing season greatly reduces the availability of nutrients present. The principal effect of both this and the lack of an A_0

[1] The first and third sets were determined by the Department of Agronomy of the Virginia Agricultural Experiment Station, Blacksburg, Virginia, through the kindness of Dr. S. S. Obenshain, Chief Agronomist. The second set was determined by the School of Agriculture, Pennsylvania State College, State College, Pennsylvania.

TABLE 2. Analysis of soil samples from: (A) The most severe part of the barren at Station 2 on the experimental area near Eagle Rock, (B) a well vegetated north slope at Station 5 of the same area, and (C) a richly wooded talus slope located below a steep barren in Botetourt County, Virginia just south of Douthat State Park.

Locality	Soil depth	Sample number	Total weight soil and rock in grams	Total weight of 20 mesh soil only, in grams	Total weight of duplicates 20 mesh soil only used for all analysis, in grams	Percent of total weight	pH	Truog phosphorus P. P. M.	Exchangeable Bases In Milli-Equivalents Per 100 Grams Soil: Hydrogen	Calcium	Magnesium	Potassium	Total cation exchange milli-equivalent per 100 gms. soil	% Base saturation	Organic matter
A Barren slope	0-3″	1	694.3	158.5	311.7	23.5%	4.55	4.8	9.63	2.85	0.93	0.25	13.66	29.50	3.6
		2	620.4	153.2											
	3-7″	3	680.4	161.2	292.7	21.7%	4.60	5.5	10.69	1.90	0.94	0.185	13.715	22.06	0.9
		4	668.0	131.5											
B. North slope	0-3″	5	409.4	211.8	396.0	50.0%	4.13	4.9	14.27	0.57	0.34	0.18	15.36	7.10	3.2
		6	382.8	184.2											
	3-7″	7	634.6	189.9	402.5	30.5%	4.22	4.7	11.52	0.94	0.46	0.19	13.11	12.13	1.6
		8	685.7	212.6											
C. Vegetated talus slope at base of barren	0-3″	9	294.5	154.3	303.6	47.4%	5.01	13.6	24.42	8.65	1.86	0.55	35.48	31.17	8.6
		10	343.4	149.3											
	3-7″	11	356.0	205.9	402.3	56.6%	4.95	8.4	21.92	8.99	1.27	0.42	32.60	32.76	7.0
		12	355.1	196.4											

horizon is on surface rooted plants, rather than on those rooted in the C horizon.

Other potential contributing factors which have not been investigated are (1) the precise nature of humification processes on the two slopes, (2) effect of high evaporative rates on accumulation in the barren soils, and (3) reduced demand resulting from sparse barren vegetation.

That the barrens do not result from unusual minerals or ions occurring in the substratum is further evidenced by the support of a normal flora by the same substratum on adjacent slopes, as well as by the healthy appearance of the barren flora.

TEMPERATURE

Direct insolation on the shale barren surface produces soil temperature gradients comparable to those of any bare surface (Daubenmire 1943). The major factors controlling maximum temperatures attained, as well as slope of the temperature gradient, are the amount of radiant energy received (this controlled by angle of incidence to the sun and interference by the atmosphere and vegetation), moisture, and soil texture, structure and color. Since most barrens are formed on moderate south facing slopes, they are exposed to sunlight for 8 to 12 or more hours per day.

On the rock mantle the maximum surface temperature measured by means of a thermistor was 63°C, but throughout the summer, surface temperatures of 55-60° C were very common during the warmer 4 or 5 hours of the day. At this time of day the surface of the dry soil falls 10-20° C within the first quarter inch, falls approximately this much again in the next three quarters of an inch, and then gradually tapers off to a temperature of about 30°C at the 4-6 inch depth. Variations of 2° to 10° C were found on irregular surfaces within spaces of less than a tenth of an inch. Fluctuations, of course, also occur in duration of time. For example, a rock fragment, cooled 8° C by shading, required six minutes to attain its original temperature of 44° C when shade was removed. Air temperature gradients withing a few inches of the surface were even steeper than those determined for the soil.

These field air and soil temperature determinations were repeatedly verified on the same soils in the laboratory, by the method described by Platt & Wolf (1950). By this means, it was possible to produce much higher ones (Fig. 17) as well as to duplicate soil and approximate air temperatures obtaining under natural conditions.

Although detailed measurements of air temperature gradients above the first few inches of the surface have not been made, two series of measurements obtained give an indication of conditions existing there. One, an indirect measurement secured by the use of

atmometers, is discussed later. The other consists of weekly maximum-minimum temperature records (Fig. 11) obtained at Stations 2 and 5 of the experimental area for five weeks during the summer of 1947. Standard Taylor maximum-minimum mercury type recording thermometers were used. At Station 2 the thermometer was hung on the shady side of an old stump in the middle of the most exposed area at a height of 30 inches, while at Station 5, on the north slope, it was placed on the shaded side of a tree at a height of 4 feet. The results would be more comparable had both thermometers been placed at the same height.

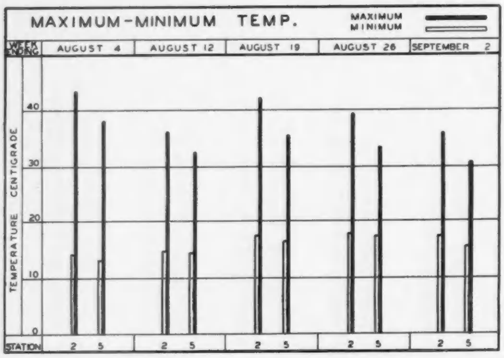

FIG. 11. Maximum-minimum temperature data for five consecutive weeks on the experimental area near Eagle Rock, summer, 1947.

Data obtained demonstrate a small but significant difference between the two stations. Weekly variations in the maximum temperature range between the two slopes was 3.5-6° C, with an average of 5.2°, while the minimum temperature varied from 0-1.5°, with an average of 1.1.° The maximum temperature attained at Station 2 within these five weeks was 43°, while at Station 5 it was 37°. Though leaf temperature measurements at these heights have not exceeded 39°, many measurements of 40-47° have been obtained in the sun only a few inches above the ground. Since but few leaf temperature measurements were obtained at a height of 2 feet, the 39° maximum is probably not significant.

Analysis of these data indicates that soil temperatures are critical only at the surface, where they are often well above the physiological tolerance of most plants. Plants growing in or through the surface fragments, at points of contact, are subject to the same temperature as that attained by the fragments. Effects of these surface temperatures would be primarily upon seed germination and seedling establishment. Air and sub-surface temperatures probably have their greatest effect upon the character of the vegetation, rather than upon its relative prevalence.

MOISTURE

One of the most striking characters of the shale barrens is their apparent lack of moisture. Even within a few hours after a heavy rain, clouds of dust may be scuffed up from the surface and the soil is uncomfortably warm to walk upon for long, even with heavy shoes. Allard and Leonard (1946) make numerous references to this apparent xeric condition, and even go so far as to say at one time that these areas are the counterpart of our western American deserts. Steele (1911), however, noted that the vegetation did not seem to reflect extreme drought. From this investigation, it is evident that sufficient moisture is retained within the soils and substrata of these barrens to support an even greater number of mature plants than naturally occur. It is primarily in the effect of the dry upper layer of soil and rock fragments on seed germination and particularly on seedling establishment that moisture becomes a limiting factor.

The moisture factor has been investigated with respect to (1) rainfall, (2) atmospheric moisture, (3) evaporation, (4) movement of water through the soil, (5) erosion and (6) soil moisture content.

Rainfall isopleths and mean annual rainfall data for the shale barren region (Fig. 8) show a rainfall of 26 to 40 inches per year. Precipitation data in Figure 9 represent the probable maximum monthly variations that occur within the region. Although rainfall distribution is fairly even throughout the twelve months of a year, a slight increase occurs generally in the three warmest months, June, July and August. Correspondingly, there are a greater number of days with rain during these summer months. The average number of days per month with more than .01 inch precipitation for Upper Tract (Fig. 9) varied from 4 to 6 for the fall and winter months and from 7 to 9 days for the spring and summer ones. At Hot Springs the corresponding variations were from 6 to 8 and 9 to 12 days. However, frequent dry spells of one to two weeks' duration occur. Weather Bureau records indicate that during the summer months about one-half of the rains, representing about one-third of the precipitation, fall as showers of but a few minutes' to a few hours' duration.

Published precipitation rates represent a higher volume of rain than that actually received by these barren areas, since an inverse relationship exists between rainfall and steepness of slope (Allard & Leonard 1946). On a vertical surface no rain would fall, and the water loss would be 100%. On a surface inclined 30 degrees, the water loss would be 13.4%, and for 45 degrees 29.3%. Thus on a 45 degree slope an annual rainfall of 26 inches is reduced to 19.4 inches, and one of 40 inches is reduced to 28.4 inches, providing all of the rain falls vertically. This would apply, of course, to both north and south slopes.

It is interesting to note that there is no evident relationship between rainfall and the degree of barrenness occurring in various parts of the region. It may be that the mean annual rainfall is a purely

coincidental factor in shale barren formation, and barrens may develop with even higher annual precipitation rates. Unfortunately, this cannot be checked.

Atmospheric moisture was measured on the experimental area near Eagle Rock by the use of standard sling psychrometers and Livingston porcelain atmometers (Livingston 1935) and equipped with mercury drop rain valves. Atmometers were calibrated before and after field use and indicated corrections were made to data obtained. Inasmuch as the barren there is enclosed on all sides by relatively dense vegetation, as it is true of the majority of barrens observed, the movement of air between the barren and adjacent areas tends to equalize relative humidities obtaining. At noontime on hot sunny days with gentle breezes, relative humidities varied from 35-45% between all seven stations, with the lowest reading occurring on the barren itself. As evening approached, relative humidities of these stations rose to fairly uniform values of 60-90%. Under unusual conditions of rainfall and air movement, much greater differences undoubtedly occur. All humidities were measured at a height of 12 inches, which is towards the maximum height of herbaceous growth.

Measurements of the evaporative power of the air, obtained by the use of atmometers (Fig. 12), are of particular importance because they integrate the influence of all the atmospheric factors that promote evaporation from the soil, and most of the external factors that affect transpiration. Of the three factors controlling the evaporative power of the atmosphere, relative humidity, temperature, and air movement, that of temperature is probably the most influential on the barrens. While gentle breezes predominate throughout the summer, and relative humidity differences as indicated above are not great, the temperature, particularly of the surface and immediately adjacent air layer, is much greater than that of surrounding areas.

To introduce the element of temperature in the atmometer data, black and white spheres were used in pairs. These were located at each of the seven

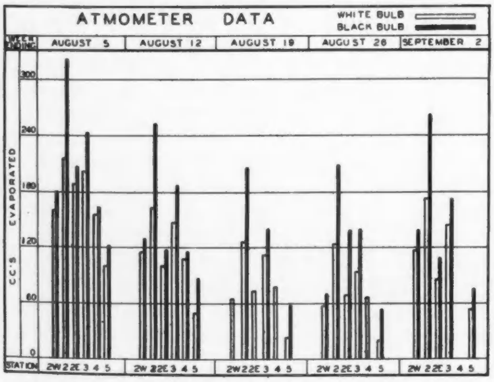

FIG. 12. Atmometer data for five consecutive weeks on the experimental area near Eagle Rock, summer, 1947.

stations, excepting No. 1, with the top of the evaporating surfaces 8 inches above ground. While at lower levels differences obtained would be much greater and at higher levels less, this elevation was chosen because it represented the average height of the herbaceous cover of the barrens. Data given in Figure 12 show not only that the evaporative power of the atmosphere over the barrens is more than double that on the north slope, but also that temperature has an even greater proportionate effect on evaporation.

In view of the yet higher evaporation rate occurring at the soil surface where temperatures are increased by 15° to 30° C or more, the rapid drying out of the surface layer of soil is easily understood. That the soil is not dried out to a greater depth than about three inches during the normal dry spells of a week or more during the summer, is due to its texture and structure. The surface layer of rock fragments, from which most of the soil has been removed by rain, passes gradually into a matrix of rock fragments and fine silt loam, which has a high water holding capacity. This surface layer, though quickly heated and therefore rapidily depleted of water, is by means of its numerous dead air pockets an excellent insulator for the silt loam below, and prevents the exposure of capillary water to wind movements and high temperatures. Because of the sparse vegetative cover, relatively little water is lost by transpiration.

To obtain a still clearer picture of water relationships on the barrens, an attempt was made to trace the course of rain water falling upon them. Water-soluble powdered dyes, such as eosin and nile blue were used as "tracers." These were placed in eight widely varying locations on the experimental barren near Eagle Rock. At each location an ounce of dye was placed either in a quarter-inch-deep contour trough six feet long and then covered, or similarly sprinkled directly on the surface. Precipitation was checked by a rain gauge made by fitting a 5 inch glass funnel to a 5 inch bottle filled with water to a mark, and then covering the water with a light oil to prevent evaporation. All locations were examined a week later, with a half inch of rain intervening. At each location the dye had coursed down the slope from 2 to 8 feet, making a solid but faded stain on the surface. Although at the line of application the dye had penetrated the underlying silt loam to a depth of one inch or more, down slope it had discolored only the surfaces of the rock fragments.

The results indicate that the initial rain water moves predominantly down slope along the surface layer of rock fragments, up to a distance of several feet. This may be roughly likened to movement of water over a shingled roof. There is a certain probability for each molecule of dye to pass by or be adsorbed on a given surface, the probability being proportional to the rate of movement of the molecule.

From water which wets the surfaces of the soil particles and therefore moves more slowly, the dye will be rather quickly adsorbed. However, the water which moves over these wetted surfaces, and therefore travels much faster, will retain its molecules of dye for a longer period of time. As additional rain falls, and mingles with the free water present, this action proceeds down the slope until all the dye is adsorbed. That this movement is a gentle one is evidenced by the remarkable stability of the surface fragments, as shown in the discussion on soils. While it was not feasible to continue this experiment under more exact conditions, it does represent a technique that may be of value in studying soil water relationships in certain habitats.

Additional studies show clearly that this type of movement does not hold for succeeding stages of rainfall. With gentle to moderate rains all subsequent water enters the soil as rapidly as it falls. During heavy showers of short duration, water may accumulate in such volume on the surface as to cause small washes. These are terminated by the up-heaping of debris which scatters the erosional stream, and permits it to enter the ground. It is only in rare cases of heavy rainstorms of long duration that pronounced gullies develop, and water is lost by run-off. On barren slopes accentuated by stream action, these conditions are modified.

Of many such observations made during and immediately after rains, one is sufficiently noteworthy to be recorded here. A sudden 25 minute thunder shower and hailstorm of unusual force occurred during the exploration of a barren 2 miles west of Millboro, in Bath County, Virginia. The lower 150 feet of this barren, with a slope of more than 50°, ended abruptly in the bed of a small stream 6 to 10 feet in width. Its surface was unusually uniform for such a slope and was rarely broken by small shale ledges. Across the stream from the barren were thinly pastured fields of the same strata. Initially, the volume of water was too great to be taken in by the soil, and for the first few minutes water coursed along the surface, infrequently producing quickly dissipated small washes. Water penetration was less in areas covered by larger rock flakes than it was in those where the surface was covered by small isodiametric fragments, or where the soil texture was particularly loose and porous. Once the soil was wetted, water was taken in as fast as it fell. During this time the fields across from the barren were literally covered by sheets of water which produced effective sheet erosion. That little water escaped from the barren was strikingly demonstrated in that, although the half of the stream adjacent to the fields was quickly muddied, that adjacent to the barrens remained perfectly clear for more than thirty minutes following the rain. At the end of this time the muddy water from the fields had diffused across the stream until the slowly narrowing clear area was eliminated.

Occasionally, areas are found on these barrens where removal of soil by erosion has left the bases of individual plants and small clumps of vegetation elevated 6 or 8 inches. Such localized occurrences are exceptional and are not considered as invalidating the general conclusions drawn above.

The question of a greater rate of sheet erosion of the barren surfaces over that of vegetated slopes can be answered only indirectly. Even a slight differential in the erosional rate would result in time in the removal of soil from the barrens, granting that the rate of soil formation is the same. Although from the dye experiments, it was seen that the initial rain water moved downwards before entering the ground, it moved chiefly along the surface fragments, rather than over the silt loam. While certainly soil particles do move downwards at an imperceptible rate, it is very questionable if this rate exceeds, on an average, that for vegetated slopes of the same formation.

Evidence has been sought also on gravitational water and on water tables. The amount of gravitational water which is held by the loose and weathered substratum, extending from a few inches to many feet below the C horizon, is largely determined by the configuration of the strata. The resulting differential ability of various barrens to hold water is correlated with density of vegetation found on them. Where barrens are formed on anticlines considerably more vegetation is found at and below the ends of the arches where seepage produces somewhat more mesic conditions than is found on the crests. Within any group of barrens the driest and least vegetated are those whose surfaces are parallel to the rock strata. In the spring of 1948 two barrens in Alleghany county were visited late one afternoon and again the next morning, with a clear cool night intervening. Although in the afternoon both slopes were dry and dusty, the next morning one was decidedly moist from seepage water while the other remained dry. The moist slope had correspondingly more vegetation.

While seepage moisture is lost from slopes only by evaporation during the summer, a considerable amount may be lost by run off in the spring when the ground is much wetter because of early thaws, accumulated rains, and lower evaporation rates. At this time small streams and wet places on and at the base of barrens are not uncommon. This water movement in the substratum affects the development of the vegetation in its influence upon the water table, and, perhaps more directly, in its effect in the spring on seed germination and seedling establishment.

To ascertain more precisely the relative moisture contents of these soils, samples were collected weekly at all stations for eight consecutive weeks during July and August of 1947 at the experimental area near Eagle Rock. The samples were conveyed to the laboratory in 8-ounce bottles fitted with moisture-proof screw caps, weighed, dried for at least 24 hours at 105° C, reweighed, and their moisture content computed. Samples were taken by soil horizons and at constant depths to ensure uni-

formity. Records for one of the driest and for one of the wettest weeks of this period are given in Figure 13, and the data are representative for the entire period sampled.

Two significant facts emerge from these data. The first is that at an average depth of 6 to 8 inches, representing the lower part of the C horizon, the moisture content for all seven stations was remarkably uniform throughout the whole series of determinations. Moisture content of the substratum was also about the same. The second fact, in contrast, is the tremendous variation which occurs in the moisture content of the upper soil layers. Since the lower layers are thoroughly wetted only by protracted rains during this season, the different water-holding capacities and particularly the evaporation rates of these upper soil layers are the primary factors responsible for these variations.

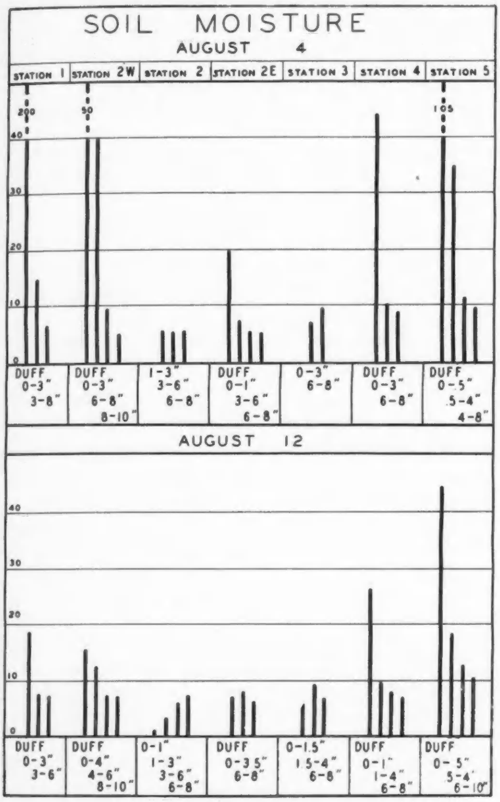

FIG. 13. Representative soil moisture percentage determinations for the experimental area near Eagle Rock, 1947. August 4th samples were collected a day following a week of dry weather. Large fluctuations occur only in the upper soil layers. Moisture content of the lower layers is relatively constant.

Although it is possible that the continued high rate of evaporation on the barrens through the summer months, along with the fairly uniform rainfall, may gradually lower the moisture content of the C horizon and of the substratum, there is little evidence in the vegetational response that this content falls below that of the wilting coefficient, except possibly in rare times of severe drought as occurred in 1930. During the three summers in which observations were made, many plants initiated new growth following heavy rains, but this was checked within a few days, if dry weather again prevailed. Wilting was infrequently observed, and evidence of death from drought was almost lacking. With respect to the more deeply rooted plants, it is quite evident that moisture retained by the lower part of the C horizon and by the substratum is not only adequate to promote growth in the spring and to sustain life in the summer, but also to support an even denser vegetational cover.

The extremely low moisture levels and correspondingly high temperatures frequently obtaining in the upper layer of rock fragments are critical, especially with respect to processses of seed germination and seedling establishment, and to growth of surface-feeding trees and shrubs. For the former, they are limiting, and for the later effective only in promoting stunted growth.

FIRE AND MAN

Scientific interest in shale barrens is generally restricted to botanists and geologists. Because of their relatively low economic value, foresters, soil conservationists, and agronomists of this region have little, if any, knowledge of them. Local residents, however, are usually familiar with those occurring in their locality, and at times visit them, because of their unique character.

On barrens of low inclination adjacent to pastured fields, cattle and goats may crop some of the low vegetation. Those adjacent to roads are sometimes quarried for road material, and occasionally the right of way for power lines cross one. The greatest disturbance by man is caused by highway and railroad construction.

The possibility that these barrens originated through lumbering can be rejected. The tree growth is unfit for lumber, and evidence of lumbering activities has not been observed. Furthermore, the history of such activities in this region precludes such a possibility. The first large scale lumbering operations took place during and after World War I, and prior to that time such operations were restricted to the immediate vicinity of settlements. Not only do the larger trees of the barrens observed antedate by far these operations, but questioning of some twenty older inhabitants ellicted no recollections of any changes occurring on these slopes within their lifetime.

The influence of fire as a causal agent in barren formation is equally negligible. Fires in this region are quite rare and localized. Since shale barren surfaces are bare and tree cover sparse, they usually escape even those fires which completely surround them. Careful examination of tree trunks gave no indication of fire sears.

THE VEGETATION

Characteristic and Endemic Species

Previous investigations of the shale barrens have been concerned primarily with the endemic and characteristic ferns and flowering plants. A discussion, along with principal literature references, of species of 38 genera has been given by Wherry (1930), and for a more restricted group by Core (1940). Allard and Leonard (1946) discussed at length some of the more interesting plants found both on and adjacent to the barrens on Massanutten Mountain, and Artz (1937) considered a more limited group for the same area.

A list of characteristic shale barren plants, based on field observations and over 900 collections, is given in Table 3.[2] The 24 species and varieties of lichens, representing collections chiefly in the southern part of the region, include 15 found directly on loose rock fragments and exposed ledges, 7 on bark of trees, and 2 which form ground mats. The 4 mosses are common in rock crevices but rarely are found elsewhere on the slopes. Though several ferns occur, only one, *Cheilanthes lanosa,* is so widespread as to be included. *Selaginella rupestris,* the only fern ally, spreads extensively where established over the drier rock ledges and loose fragments.

The 97 species and varieties of flowering plants include only those occurring on the most exposed areas. Species of a weedy nature, such as common mullein, ragweed, etc., are excluded, as are in general those which appear sporadically.

Nineteen flowering plants may be regarded as indicator species. Eight, as follows, are considered strict shale barren endemics:

Aster lowrieanus
Arabis serotina
Clematis albicoma
Clematis viticaulis
Eriogonum alleni
Oenothera argillicola
Solidago harrissii
Trifolium virginicum

Another nine which are native to the mid-Appalachians and occur most frequently on shale barrens are:

Allium oxyphilum
Antennaria virginica
Antennaria virginica var. *argillicola*
Arabis laevigata var. *burkii*
Clematis albicoma var. *coactilis*
Convolvulus purshianus
Phlox buckleyi
Pseudotaenidia montana
Senecio antennariifolius

The remaining two, *Astragalus distortus* and *Viola pedatifida* (Platt 1950), although native to the mid-western prairies, have a disjunct range extension in this area, the former known chiefly and the latter known only from barren areas.

Allard and Leonard (1946) compared the flora of the Massanutten shale barrens with that of other areas showing "similar narrow limitations of ecological diversity" on the basis of generic coefficients, $\frac{\text{No. genera}}{\text{No. species}} \times 100$. Their list of 287 entities (published in part and including not only characteristic shale barren plants, but also many species of adjacent habitats), represent 172 genera, and give a coefficient of 59.9%. They compare this on the one hand with a coefficient of 74.7% for Dodge's *Flora of Point Pelee,* representing a uniform area of wet sandy marshes, and on the other hand with a coefficient of 23% for Small's *Flora of the Southeastern United States,* and 31.2% for Core's *List of Vascular Plants of West Virginia,* both of which represent areas of great ecological diversity. The characteristic plants in Table 4 have a generic coefficient of 64.6.% Although this percentage does not represent the entire flora, it is indicative of the relatively uniform ecological conditions obtaining on the barrens.

Mature Plants

As the investigation of environmental factors developed, it become evident that the environment of the C horizon is impressed chiefly upon the processes of growth and seed production of well established and mature plants. The environment of the upper layer of rock fragments is imposed chiefly upon the processes of seed germination and seedling establishment. Therefore a discussion of vegetational response may be logically developed along these two lines.

LIFE FORMS

One method of indicating vegetational response of

[2] Dr. John W. Thompson, Jr. of the University of Wisconsin kindly made the lichen determinations, Dr. Edwin T. Moul of Rutgers University the mosses, and Dr. Richard W. Pohl of Iowa State University the grasses. Nomenclature of the ferns and flowering plants, except as noted below, is in accordance with Gray's Manual of Botany, Eighth Edition. In this edition, Professor Fernald neither recognized shale barrens as unique plant habitats, nor correspondingly, the existence of shale barren endemics. Habitats of the endemics he included in the Manual are given simply as "shaly slopes," "dry rocky slopes," or "dry shales," and their distribution is generalized. One strict endemic, *Arabis serotina* Steele, is omitted from the Manual and two others most frequently occurring on the barrens, *Allium oxyphilum* Wherry and *Convolvulus purshianus* Wherry are reduced to a form and an intermediate respectively. Three species and varieties well known on the barrens also omitted from the Manual are: *Liatris spicata* (L.) Willd. var. *montana* Gray; *Aster oblongifolius* Nutt. var. *orientis* Shinners; and *Helianthus reindutus* (Steele) Fernald. It may be added that there is reason to expect that further taxonomic study will result in changes in a few names of shale barren plants as adopted in the Manual, as for example in the case of "*Clematis albicoma* var. *coactilis*" which does not appear to be closely related to *C. albicoma*. Specimens of all these plants are either in the Herbarium of the University of Pennsylvania or that of Emory University.

TABLE 3. Plants characteristic of the more exposed areas of the shale barrens.

Lichens	
Crocynia lanuginosa	Shale
Diploschistes scraposus	Shale
Leptogium chloromelum	Shale
Lecidea lucida	Shale
Cladonia rangiferina	Mats on ground
Cladonia subtenuis	Mats on ground
Cladonia mitis	Shale
Cladonia pyxidata var. *neglecta* f. *simplex*	Shale
Cladonia cristatella f. *ramosa*	Shale
Lecanora cinerea	Shale
Candelariella vitellina	Shale
Parmelia caperata	Bark, Juniper, Ch. Oak
Parmelia conspersa	Shale
Parmelia conspersa var. *isidiata*	Shale
Parmelia furfuracea	Bark, pines
Parmelia saxatilis	Shale
Parmelia trichotera f. *trichotera*	Bark, Pine and Ch. Oak
Cetraria atlantica	Bark, Juniper
Cetraria ciliaris	Bark, Juniper, Pine
Usnea pensylvanica	Bark, Chestnut Oak
Caloplaca elegans	Shale
Physcia orbicularis f. *rubropulchra*	Bark, Ch. Oak
Physcia subtilis	Shale
Anaptychia speciosa	Shale
Mosses	
Atrichum macmillani	Rock crevices
Polytrichum piliferum var. *hyperboreum*	Rock crevices
Grimma spp.	Rock crevices and trees
Aulocomnium heterostichum	Rock crevices
Fern Allies	
Selaginella rupestris	Exposed ledges
Ferns	
Cheilanthes lanosa	Exposed slopes and ledges
Flowering Plants	Life Forms*
Pinus virginiana	P
Pinus echinata	P
Juniperus virginiana	P
Danthonia spicata	H
Deschampsia flexuosa	H
Andropogon scoparius	H
Panicum fasciculatum var. *implicatum*	H
Cyperus filiculmis	H
Carex pensylvanica	H
Commelina erecta	G
Commelina erecta var. *angustifolia*	G
Allium cernuum	G
Allium oxyphilum	G
Polygonatum biflorum	G
Quercus prinus	P
Quercus rubra	P
Quercus ilicifolia	P
Quercus marilandica	P
Comandra umbellata	G
Eriogonum alleni	H
Polygonum tenue	T
Paronychia fastigiata	T
Paronychia fastigiata var. *pumila*	T
Paronychia virginica	H
Silene caroliniana var. *pensylvanica*	G
Clematis albicoma	G
Clematis albicoma var. *coactilis*	G
Clematis viticaulis	G
Sassafras albidum	P
Sassafras albidum var. *molle*	P
Draba ramosissima	H
Arabis lyrata	H

TABLE 3—Continued

Arabis laevigata var. *burkii*	H
Arabis serotina	H
Sedum glaucophyllum	H
Sedum telephioides	H
Spirea corymbosa	P
Amelanchier arborea	P
Crataegus uniflora	P
Crataegus intricata var. *straminea*	P
Potentilla canadensis	H
Potentilla simplex	H
Rosa carolina	P
Cercis canadensis	P
Trifolium virginicum	H
Tephrosia virginiana	G
Astragalus distortus	G
Lespedeza procumbens	G
Clitoria mariana	G
Euphorbia corollata	G
Rhus copallina	P
Rhus aromatica	P
Ceanothus americanus	P
Parthenocissus quinquefolia	G
Hypericum spathulatum	P
Viola pedata	H
Viola pedata var. *lineariloba*	H
Viola pedatifida	H
Oenothera argillicola	H
Taenidia integerrima	G
Pseudotaenidia montana	G
Vaccinium stamineum	P
Vaccinium vacillans	P
Asclepias tuberosa	G
Convolvulus purshianus	G
Phlox buckleyi	H
Phlox subulata var. *brittonii*	H
Isanthus brachiatus	T
Hedeoma pulegioides	T
Cunila origanoides	G
Penstemon canescens	H
Houstonia longifolia	H
Houstonia tenuifolia	H
Campanula divaricata	G
Eupatorium sessilifolium	G
Kuhnia eupatorioides	G
Liatris spicata var. *montana*	G
Liatris scariosa	G
Solidago bicolor	G
Solidago erecta	G
Solidago nemoralis	G
Solidago harrissi	G
Aster laevis	G
Aster pilosus	G
Aster oblongifolius var. *orientis*	G
Aster lowrieanus	G
Antennaria neodioica	H
Antennaria plantaginifolia	H
Antennaria virginica	H
Antennaria virginica var. *argillicola*	H
Silphium compositum var. *reniforme*	G
Parthenium integrifolium	G
Helianthus divaricatus	G
Helianthus reindutus	G
Coreopsis verticillata	G
Senecio antennariifolius	H
Hieracium venosum	H
Hieracium greenii	H

*Indicates the life form according to Räunkiaer's classification, as given below

	Total for each Life Form
T—Therophytes: annuals	5
G—Geophytes: perennating organs underground	40
H—Hemi-cryptophytes: perennating organs just above ground, but protected by leaf rosettes	31
P—Phanerophytes: aerial plants, perennating organs more than 10 inches above the ground	21
	97

mature plants is a study of "life forms," the forms which the vegetative bodies produce as the result of all life processes which are affected by environment. This brings together those organisms which in their entirety show similar morphological adjustments to the environmental complex independent of their taxonomic position. The characteristic flowering plants have been classified according to Räunkiaer's (1934) system of life forms (Table 3), a system based primarily on the adjustment of plants to the unfavorable season, as indicated by the location of perennating organs.

Of the total of 97 plants examined, 5 are therophytes or annuals; 21 are phanerophytes, trees and shrubs with perennating organs more than 10 inches above ground; 40 are hemi-cryptophytes with perennating organs just above ground but protected by leaf rosettes; and 33 are geophytes, with perennating organs underground.

The winter season, with which these life forms are correlated, is a temperate one, with the average temperature of the coldest month above −3°C. An indication of temperature extremes is afforded by the 33 year weather record for Upper Tract, Pendleton County, West Virginia, during which time the lowest was −16° C and the highest 26° C (Fig. 9). In this area snow cover is intermittent, and alternate freezing and thawing of the upper 5-15 cm of the ground in which the perennating organs of the geophytes are located is frequent. Since a search for effects of frost-heaval has been fruitless, this factor is presumed to be negligible. The elastic and deep seated root systems of the herbaceous perennials must afford some protection in this respect.

Field and laboratory observations indicate that the perennating organs of these plants are well adapted to survival of winter conditions. A field examination was made of these organs on two barrens and adjacent areas on April 1, when a few were yet dormant and the others had initiated spring growth. Although the geophytes were checked by the number of new shoots with respect to the dead stalks of the previous year, the soil was removed from 20 of them as a precautionary measure. The evidence was so overwhelmingly in favor of winter survival for all types of perennating organs that further observations were deemed unnecessary. Of 35 pots of plants which had been placed in cold frames over winter at the laboratory, only 3, which were small and poorly established, failed to survive.

Since the winter immediately concerned was comparatively mild, these observations do not indicate responses to climatic extremes.

ROOT-SHOOT RATIOS

Summer conditions on the barrens are probably much more difficult for the nature plants than winter ones. Of these, conditions of the soil in which plants are rooted are most critical. One method of obtaining a relationship between plants and soil is by the determination of "root-shoot ratios"; i.e., a visual estimate of the relative size and extent of the root system with respect to that of the shoot.

The ratios can be roughly divided into three groups which exhibit a positive correlation with life forms. The 5 therophytes (annuals) have fibrous root systems approximately equivalent to their aerial parts, the 21 phanerophytes (trees and shrubs) have root systems tending to be proportionately smaller and less effective in relation to requirements of the shoot for increased growth, while the 33 geophytes and 40 hemicryptophytes (all perennials) have root extensions much larger than those of their shoots.

The significance of these ratios is resolved not only on the assumption that the larger the root with respect to the shoot the greater the ability of the plant to survive adverse summer conditions, but also on the location of the root systems with respect to themselves and to the soil.

GEOPHYTES AND HEMI-CRYPTOPHYTES

The 73 perennials in these categories have root systems much larger than their shoots. Although considerable variation occurs in respect to initiation of spring growth, time of fruiting, physiological tolerances to growth conditions, etc., these plants hold other characteristics in common which are probably much more significant in their ability to grow on the barrens. In addition to life forms and root-shoot ratios, all are rooted in the C horizon, and all, in general, are widely spaced from each other (Fig. 14).

FIG. 14. A clone of *Senecio antennariifolius* near the edge of a barren, demonstrating characteristic sparsity of plant cover.

It was shown in the investigation of the environment that the C horizons of the barrens are equivalent to those of well vegetated areas with respect to moisture, nutrients, structure, texture, and depth. The barrens differ from these areas by a replacement of the normal A and leaf mold horizons with a surface mantle of rock fragments. Although on well vegetated areas, most plants are dependent to some extent upon these upper horizons for moisture and nutrients, such is not the case with the geophytes and hemi-cryptophytes, which are seemingly adapted for dependence on the C horizon alone. The general adequacy of the C horizon for these plants is well demonstrated, not only by reasons given above, but also by the rare occurrence of wilting, even on the hottest and driest days, and by the healthy appearance of the plants, including no observable nutrient deficiency symptoms. Furthermore, plants entering the barrens from other areas do so without evident change.

Many of these species demonstrate a growth response to seasonal soil moisture levels. A majority have their principal growth in the first 6 to 8 weeks of the growing season, when moisture levels are highest. During July and August almost all of them are either already dormant, having flowered and produced fruit; are engaged in a long period of seed maturation; or are continuing to produce flowers and fruit with very little increase in vegetative growth. During long wet spells some buds may initiate weak growth.

There is, of course, a relationship between available moisture and growth as demonstrated by the infrequent occurrence of plants with small leaves and no flowers, but with root systems equivalent to plants several years of age.

A detailed discussion of the root systems of these plants is hardly justified by the nature of this paper. An indication of their features is afforded by Figure 15. Artz (1937) has described the root systems of several of the more characteristic plants, and the root systems of all may be observed from the herbarium specimens. It should be pointed out that in stating these plants are rooted in the C horizon, this includes the extensions of the C horizon into the interstices of the underlying and less weathered substratum for a depth of many centimeters.

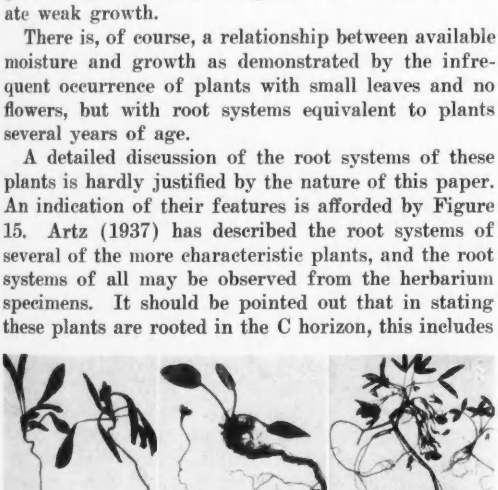

FIG. 15. Photographs of herbarium specimens of three species with tap-root systems demonstrating typical root-shoot ratios. Left: established *Oenothera argillicola* seedlings. Center: an *Eriogonum alleni* seedling and an immature plant one year old. Right: a *Trifolium virginicum* plant one year old and a mature one probably four or more years old. Left and center are one-sixth and right is one-twelfth natural size.

THEROPHYTES

The five therophytes or annuals, with approximately 1:1 root-shoot ratios, are also rooted in the C horizon. These are all relatively small plants, usually less than 15 cm in height. In general, mature plants are restricted to more favorable areas. They are not found where conditions are most adverse, even when numerous geophytes and hemi-cryptophytes are present. Evidently, their more shallow and less extensive root systems constitute at least one factor in this restriction. Probably of greater initial significance is that even if many did become established during a particularly favorable season, they could not persist throughout succeeding less favorable seasons, as is the case with perennials.

PHANEROPHYTES

The 21 phanerophytes, trees and shrubs, have root systems which become proportionately smaller and less effective as the growth demands of the shoot increase with age. This conclusion is based on observations of the growth rates of the plants concerned.

Forty-three measurements of growth rate were made of the woody species found at Stations 1, 2, 2E, 4 and 5 of the experimental area near Eagle Rock. Age was determined by annual-ring counts, employing an increment borer for the larger trees and cutting for the smaller ones. In this region it is quite rare for a tree to make more than one growth ring per year, and the number of rings is therefore considered to approximate the actual age. Diameters were obtained by direct measurement, and heights by measurement in smaller plants and by estimate in the larger ones.

Measurements of 16 of these plants, selected to show the range of variation observed on Stations 2, 4, and 5, are given in Figure 16. These are so plotted on a triangle that the more squat the triangle, the more stunted the growth. For example, on Station 2, a juniper 300 years old was only 15 feet high, and an oak 108 years old was only 6 feet high. On the other hand, a hickory 120 years old was 40 feet high. The older shrubs fare no better, for a redbud 16 years old was only 6 feet. In contrast, growth rates at Station 5 on the north slope are several times greater.

Of further interest is the fact that the growth rings are mostly relatively uniform over long periods, thus indicating a similarity in environmental conditions throughout their life span.

In old age, trees are invariably extensively rotted until only small strips of functional xylem and phloem connect the scattered live branches with the few remaining viable roots. This condition necessitates an indirect method for age determination. Examination of the existing heart and sap wood shows that the average growth rate is equivalent to one inch of wood

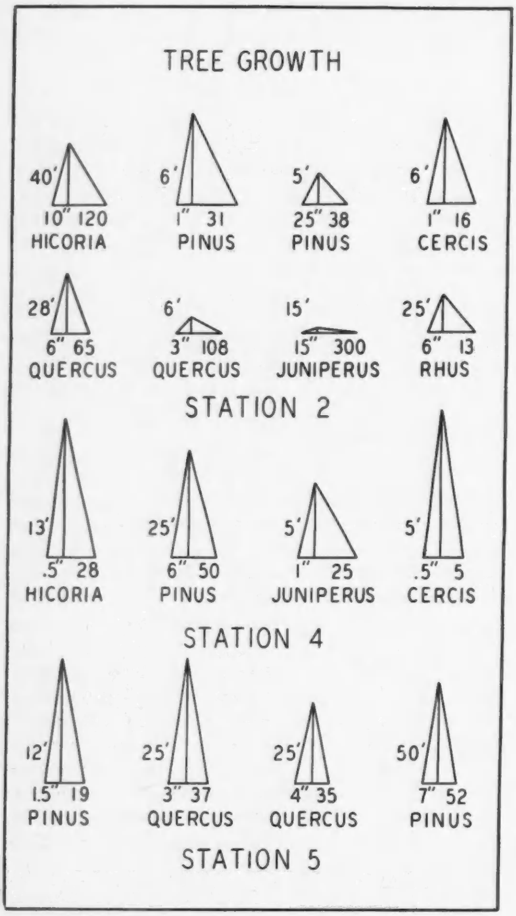

FIG. 16. Diagrammatic representation of tree growth, typical for Stations 2, 4, and 5 of the experimental area near Eagle Rock. The left axis, representing diameter, is a constant. The right axis, representing age, is determined by dividing age by diameter x 8. The vertical axis, representing height, is determined by dividing height in feet arithmetically by diameter. Thus the more squat the triangle, the more stunted the growth.

every 40 to 70 years for juniper, and slightly less for chestnut oak. Many of the junipers have a maximum diameter of 15 to 20 inches, chestnut oaks 20 to 25 inches. If a growth rate of one inch of new wood per fifty years is assumed, the ages of these older trees, from 15 to 30 feet in height, range from 350 to 500 years. By direct count, a sassafras tree 7 feet high was well over 100 years in age.

Retardation of growth in these plants is an evident result of low moisture conditions for several reasons. The plants are rooted in the C horizon, and in its extensions deep into the rock crevices. For young plants, this seems to provide adequate conditions. However, with increase in size, and corresponding need for increase in the number of surface feeder roots, this is no longer the case. On normal slopes these feeder roots have the moisture of the C, A, and leaf mold horizons, while on the barren slope, they have only the C horizon to draw from. Therefore, though the barren slope is adequate for the smaller phanerophytes, it lacks not only the moisture but as a consequence the available nutrients per unit area necessary for normal growth of the larger ones. As would be expected, intergradations of these conditions occur. Also, stunting is more pronounced on backbone ridges and otherwise drier areas than on the more favorable ones.

Despite stunting and loss of vigor in the older plants, it is of further significance that a negligible percent of them die in early maturity. Principal growth occurs, as in the perennials, during the first 6-8 weeks of the growing season, with additional spurts limited to protracted rainy spells.

SEED GERMINATION AND SEEDLING ESTABLISHMENT

Observations made on a trip to about 15 shale barrens in southwest Virginia on April 1, 1948 indicate that in general seed germination begins after many of the established plants have begun spring growth. At this time only a few scattered seedlings were observed, the oldest having developed the first two or three true leaves. However, many Clematis plants were up several centimenters and some were flowering. *Senecio antennariifolius, Trifolium virginicum, Arabis lyrata, Viola rafinesquii* and others were in late bud, and the early woodland plants such as *Cornus florida, Amelanchier* sp., *Phlox subulata, Dentaria* spp., *Anemone* spp., and *Sanquinaria canadensis* were in full bloom. The woods and fields were wet from spring thaws and recent heavy rains, and the run-off of ground water by open seepage was evident everywhere, including shale barren areas. Surfaces of the barrens dried out quickly on sunny days, and the surface temperature, warm to the touch, was estimated to be about 45° C. Nowhere, however, were the surface conditions so severe as to cause widespread injury to the seedlings.

Two weeks later, when the same barrens were revisited, the number of seedlings was estimated to have at least doubled on the exposed slopes. Surface conditions were somewhat more severe, and some seedling injury was evident.

The high temperature and low moisture conditions on these same slopes were much more adverse when visited for a third time on June 14-15. Only a few of the seedlings had become established, and new ones were difficult to find. Maximum surface temperatures, as measured by a thermistor, exceeded 60° C. Because of the increased evaporation rate, the surface dried out more quickly and to a greater depth than it had in early spring. From observations made the previous summer, a further drastic decrease in the number of established seedlings was indicated as the season advanced.

SEED GERMINATION

Frequency of seed germination in a given area is

initially determined by the number and viability of seed produced, and by the germination requirements peculiar to each species present. Since endemic species most accurately reflect in their character the ecology of the area, attention was focused on the germination requirements of several which thrive best in the most exposed areas of the barrens—*Oenothera argillicola, Eriogonum alleni, Trifolium virginicum* and the 3 species of *Clematis.* Two plants of less restricted occurrence also included were an annual, *Paronychia fastigiata* var. *pumila,* and a perennial, *Draba ramosissima.*

Dr. Lela V. Barton of the Boyce Thompson Institute made a study of the pre-germination temperature requirements of seeds of all these species, and a brief summary of her results are presented. Seeds were placed either in a mixture of sod soil, granulated peat moss, and sand in green house flats, or in granulated peat moss contained in small vials. *Trifolium virginicum* seeds were not affected by temperature, and 100% germination was obtained when the waterproof seed coats were broken. Though some seeds of *Eriogonum alleni* and *Oenothera argillicola* germinated at once, the percentage increased with daily alternating temperatures similar to normal fluctuations occurring on shale barrens in early spring. Germination percentages for seeds of *Draba ramosissima* increased both with low temperature pretreatment and with daily alternating temperatures. The seeds of *Paronychia fastigiata* var. *pumila* did not germinate at all without daily alternating temperatures, and then gave but 2 to 6% germination. Clematis seeds showed 4 to 58% germination only after low temperature pretreatment. By keeping Clematis seeds out-of-doors in peat moss for a period of 22 months, the author was able to demonstrate a secondary epicotyl dormancy, in that the root developed the first spring, while the shoot did not develop until the second spring. This was later confirmed by Dr. Barton.

Other experiments gave an indication of conditions affecting germination within the upper layer of shale soil. Seeds of *Oenothera argillicola* and *Eriogonum alleni,* when placed on moist filter paper in petri dishes at room temperature germinated 50-80% within two weeks. However, seeds of the same lot planted in greenhouse flats at a depth of ½ cm in silt loam and watered daily failed to germinate in nine weeks. Since the soil rapidly dried out after watering, moisture was suspected of being the limiting factor. Therefore, seeds of the same lot were planted in shale barren soil at a depth of 2 cm in 6-inch greenhouse pots and watered daily. An average of less than 1% seedlings were observed at the end of six weeks. Examination showed that an estimated 15% of the Eriogonum seedlings had germinated but failed to penetrate the covering scil. The pots were then treated as indicated in Table 4. Results indicate shallow planting in a loose well aerated soil, and a moisture content higher than that occurring in the

TABLE 4. Germination Experiments with *Eriogonum alleni* and *Oenothera argillicola.*

Pot Number		1	2	3	4	5	6
Percent Seedlings Visible	*Eriogonum alleni*	4	14	15	0	0	0
	Oenothera argillicola	20	15	21	0	0	0

Explanation: 100 seeds were planted in each six inch pot at a depth of 2 cm., then placed in the greenhouse and watered daily. When less than 1% seedlings were visible in six weeks, the pots were treated as follows, and the results were tabulated 3 weeks later.

Pot No. 1: Soil loosened but not mixed, covered with glass and watered from below.

Pot No. 2: Top 2 cm. of soil removed, next 2 cm. loosened, mixed, covered with glass, and watered from below.

Pot No. 3: Top 2 cm. of soil removed, next 2 cm. undisturbed, covered with glass, and watered from below.

Pot No. 4: Soil not disturbed, covered with glass, and watered from below.

Pot No. 5: Top 2 cm. of soil removed, next 2 cm. undisturbed, not covered with glass, but watered as usual from above.

Pot No. 6: Soil undisturbed, not covered with glass, but watered as usual from above.

surface layer of the barrens except during the early spring or protracted rainy spells, are necessary germination requirements for these two species.

Although it was not feasible to make direct field observations on seed germination, studies on seedling establishment afford excellent indirect evidence on this point.

SEEDLING ESTABLISHMENT

The establishment of seedlings is dependent upon adequate conditions of moisture, temperature, oxygen, nutrients, and light. Of these, moisture and temperature are the most variable and the most critical. Seedling production on the barrens is practically limited to early spring when these conditions are most favorable. That the majority of the seedlings produced at this time become temporarily established is evidenced by development of several stem leaves.

Table 5 records the relative abundance of seedlings found on three successive dates in the spring of 1948, and Table 6 a floristic and ecological analysis of seedlings collected on April 17-18. These seedlings were preserved wet on collection, carried to the laboratory, and examined under binoculars. Conclusions based on these quadrat studies are so clear cut that the inclusion of a larger number of quadrats was not warranted.

Habitats were selected to represent the more severe conditions obtaining. Sizes of quadrats used indicate the relative abundance of seedlings present; the

TABLE 5. Representative densities of seedlings observed on shale barrens on successive dates in Spring 1948.

a. By species (only areas of initial high density selected).

Species	Surface conditions	Total area, sq. meters	Number of Seedlings		
			April 1-2	April 15-16	June 14-15
Clematis albicoma var. *coactilis*	Ecotone, some shade and leaf litter	0.25	15	14	0
Pinus sp.	Ecotone, some shade, no leaf litter	0.33	15	13	0
Pinus sp.	Exposed bare slope	3.00	40	..	1
Pinus sp.	Same, but 50% shaded by cut pine boughs	3.00	40	..	6
Oenothera argillicola	Exposed bare slope	0.01	..	65	0
Oenothera argillicola	Exposed bare slope	0.02	..	80	0
Paronychia sp.	Shaded ledge, some humus	0.33	..	63	13
Eriogonum alleni	Exposed bare ledge	0.01	..	13	0
		0.01	..	23	0
		0.01	..	30	0

b. By quadrats, selected to show variation.

Surface conditions	Total area, sq. meters.	Estimated Number of Seedlings	
		April 1-2	June 14-15
Bare exposed slope, some seepage moisture..........	225	35,000	8
Ledges, some shade and leaf litter................	18	6,000	0
Partially shaded dry bare slope................	450	30	0
Exposed rough slope, open plant cover...............	18	500	20
Crevices, thick ledges........	36	40	0

smaller the quadrat, the greater the number of seedlings present in that general area of the barren sampled.

Data in these tables show a correlation between relative moisture conditions and density of seedlings present. More were in association with mature plants than not, more in flattish areas and niches than on slopes, and more in shade than sun. See, for example, averages for habitat types in Table 6. While these relative densities are due in part to seed distribution, selection of quadrats was such as to minimize this effect, at least to the point that it does not invalidate the general conclusions as to the import of the moisture factor.

Of further significance is the relatively small number of species collected. Including the unidentified, only about 20 entities were observed, and less than half of these were represented by a large majority of seedlings found. The scattering of species through the various quadrats reflect the scattered occurence of the characteristic shale barren plants.

Seedlings collected were small, the most mature having developed but 4 stem leaves. The average stem length, from seed to shoot apex, varied for different species from 1.70 to 4.10 cm. with an overall average of 2.7 cm. Although data obtained on root length are not adequate for inclusion in the table, measurements obtained varied from 1 to 4 cm.

Average seed depth varied for different species from 0.84-1.60 cm., with an over all average of 1.1 cm. The depth to which seed penetrates the soil is afforded indirectly by another observation. Rock fragments of about the same size as these seeds, but of greater density, and marked with white paint, worked into the soil over winter to an average depth of about 1 cm. and to a maximum depth of about 3 cm.

A few experimental plantings on two shale barrens produced essentially the same results (Table 7) as obtained from the investigation of seedling establishment under natural conditions. From 800 seed planted in mid April, only 25 stunted, damaged, or rotted seedlings were evident 2 months later, and these were of domestic plants—sorghum, corn, and bush limas. Continued observations throughout the experiment being impractical, it was not possible to determine definitely why so few seedlings were obtained. Besides the adverse conditions for germination and growth, some, as for example corn, may have been destroyed by rabbits or deer.

The above evidence indicates that both seed germination and seedling establishment must occur in the surface layer of rubble where moisture conditions are inadequate for plant growth, except in the early spring or possibly during protracted rainy spells later on. However, no seedlings were observed after May, and very few after April.

CAUSES FOR SEEDLING MORTALITY

Each of the 261 seedlings in Table 6 were placed in F.F.A. solution on collection, and then examined for signs of injury in the laboratory by means of a binocular. Since almost all of the injuries were caused by high surface temperatures of the rock fragments, these were the only ones recorded. It was estimated that only about 5% had been damaged mechanically or by insects. Burn injuries ocurred in 25-76% of the seedlings in each quadrat, and 0-70% in representative species. All seedlings were small, the oldest having only 4 seed leaves.

TABLE 6. Ecological and floristic analysis of seedlings collected April 17-18, 1948. (Seedling measurements in centimeters, quadrats in square meters.)

A. Analysis by habitat types.

Habitat types	TYPE A*		TYPE B		TYPE C				TYPE D	
Quadrat designations	Douthat	Goshen	Douthat		Brandywine		Goshen		Millboro	Totals and Averages
	No. 3	No. 8	No. 1	No. 2	No. 4	No. 5	No. 6	No. 7	No. 9	
Quadrat size	0.2	0.4	3.3	3.3	450	2.2	1.1	3.3	18	
Species and number of seedlings										
Pine	1	....	3	13	11	4	....	....	1	33
Eriogonum alleni	6	22	1	2	....	7	12	4	8	62
Oenothera (?)	....	....	2	....	....	21	9	....	....	32
Clematis spp.	7	2	1	....	....	....	....	....	....	10
Grass	7	....	5	....	....	....	3	....	....	15
Ambrosia artemisiifolia	7	....	3	....	....	....	....	....	....	10
Polygonum sp.	1	....	1	....	....	....	....	....	....	2
Polygonum tenui	....	12	3	....	....	....	6	....	5	26
Houstonia (?)	5	....	9	....	2	....	....	....	....	16
Trifolium virginicum	2	....	1	....	....	....	....	....	....	3
Tephrosia (?)	....	....	....	....	....	....	....	....	5	5
Cunila (?)	....	....	7	....	....	....	....	....	....	7
Unidentified	7	6	4	....	2	3	4	4	10	40
Totals	43	42	40	15	15	35	34	8	29	261
Species per quadrat	9	5	14	3	3	4	5	2	6	5.7
Seedlings per sq. m.	215.0	105.0	12.2	4.5	3.3	15.9	30.9	2.4	1.6	43.4
Species per sq. m.	45.0	12.5	4.2	0.9	0.007	1.8	4.5	0.6	0.33	7.7
Average seed depth	1.	1.1	1.3	1.6	1.3	1.	.8	1.1	.8	1.1
Average stem length	2.4	3.	2.6	3.1	3.8	2.3	1.7	2.5	3.0	2.7
Damaged by heat	31%	44%	25%	63%	53%	41%	41%	37.5%	76%	45.7%
Averages for habitat types:										
Seedlings per sq. m.	160.0		8.4		13.1				1.6	
Species per sq. m.	28.7		2.5		1.7				0.33	
Average seed depth	1.5		1.45		1.05				.8	
Average stem length	2.7		2.8		....				3.0	
Damaged by heat	37%		44.0%		43.0%				76%	

*Type A: Mature herbs present, seepage moisture available, surface broken by small ledges, 1 to 5 cm. mantle of rock fragments.
Type B: No mature herbs present; seepage moisture available; surface smooth; 1 to 5 cm. mantle of rock fragments.
Type C: No mature herbs present; no seepage moisture available; surface smooth; 1 to 5 cm. mantle of rock fragments.
Type D: Scattered mature herbs; no seepage moisture available; surface flat, smooth, and covered by a 10 cm. mantle of fine cinders from train smoke.

B. Analysis by representative species.

	Pinus sp.	*Polygonum tenue*	*Houstonia* ?	*Eriogonum alleni*	*Clematis* spp.	Grass	*Ambrosia artemisiifolia*	*Trifolium virginicum*
Average seed depth	1.43	1.13	1.10	1.06	1.40	0.84	1.30	1.60
Average stem length	3.71	3.09	2.70	2.74	3.10	2.80	3.20	4.10
Damaged by burning	70.6%	57.7%	62.5%	60.4%	0.0%	7.0%	36.0%	0.0%
Total number of seedlings	33	26	16	32	10	15	10	3
Number of quadrats represented	6	4	3	8	3	3	2	2

The sharp temperature gradients occurring in the surface layer of the barrens have been noted above. Burn injuries in the seedlings are correlated with the frequency, duration, and maxima of temperatures attained, and by the relative hydration and temperature tolerance of the seeding tissues. These conditions, in turn, are correlated with exposure and soil moisture. For example, Clematis and Trifolium seedlings, with no recorded injuries, were well shaded by mature plants and located in areas with relatively higher soil moisture levels than were seedlings of Pinus and Polygonum which were located, for the most part, in exposed and well drained areas.

Laboratory studies were made of the effect of radiant energy on seedling survival, and indirectly of its effect on moisture levels in the upper soil layers,

TABLE 7. Experimental plantings on shale barrens.

Seeds planted April 16-17	Seedlings present, June 14-15
Eagle Rock, exposed slope	
75 Sorghum	3
25 Sunflower	0
200 White Clover	0
100 *Oenothera argillicola*	0
50 Corn	3
50 *Pinus rigida*	0
Douthat, exposed slope	
50 *Pinus rigida*	0
25 Sunflower	0
100 *Oenothera argillicola*	0
25 Corn	13
25 Bush limas	6
Douthat, shaded level place, some leaf litter	
25 *Pinus rigida*	0
50 *Oenothera argillicola*	0
800	25

using the technique described by Platt and Wolf (1951) (Fig. 18). In this technique, natural soil temperature gradients are experimentally controlled by the application of radient energy from infra-red lamps to pots of seedlings, which in turn are rotated on a table to provide more uniform conditions. Approximately 300 seedlings each of *Pinus rigida* and *Oenothera argillicola* were obtained in a total of 16 pots. All seed were planted at a depth of 1 cm and the seedlings, when tested, were 1-3 cm high, with only the cotyledons developed. Pine seedlings were in eight 7-inch pots containing finely divided coal and black shale, while the Oenothera and Eriogonum seedlings were in eight 5-inch pots containing shale barren soil, covered with a .5 cm layer of small shale fragments. All pots were soaked, allowed to drain, and then placed in 5 cm deep containers filled with water.

Surface temperatures varying from 43-80° C were maintained for periods ranging from 2-7 hours. Temperatures, as indicated by a thermistor, were obtained of the stems of 56 seedlings, distributed in 6 pots, at their points of contact with the surface. In others, only the maximum surface temperatures attained were recorded. The coal surface remained moist, except at the higher temperatures, but the shale soil quickly dried out through the entire temperature range. The only damage observed to the seedlings was burn injury at point of contact with the surface. Under these conditions, the majority of burns occurred at 52° C and above. The lowest at which injury occurred for an individual seedling was 46° C and the highest attained before injury was 54° C. The data are not extensive enough to be analyzed for correlation of damage with duration of temperature, or with moisture content of the soil or plant tissue. They are adequate, however, to show that for two shale barren plants, seedlings cannot generally withstand surface contact induced temperatures of 52° or above.

DISCUSSION

These observations and experimental data on shale barren vegetation again confirm the lithological character of the substratum as the primary causal factor in the formation and continuation of shale barrens. This factor, under the stated conditions of slope and exposure, is responsible for the unique development of the soil, in which the normal A and leaf mold horizons are replaced by a surface layer of rock fragments. These conditions in turn are correlated with the character of the vegetation. Geophytes and hemicryptophytes, whose root systems are relatively independent of a rich moist surface layer, can grow satisfactorily. Other plants, particularly trees and shrubs, whose root systems are dependent upon such a surface horizon for normal growth, demonstrate severe stunting. However, all of the mature plants are generally adapted to survive the adverse conditions of both winter and summer. The survival rate is such that it does not constitute a direct causal factor for the sparsity of plant life on the barrens.

From seed germination studies, it is clear that unusual limitations on the amount of vegetation are not imposed either by the number, distribution, and viability of seed produced or by the climatic conditions required to break the various kinds of seed dormancy represented. However, the high temperature and low moisture conditions of the surface layer are so severe as to sharply curtail seedling establishment. This then constitutes the critical point in plant growth, and is the factor responsible for the sparsity of plant life on the barrens.

THE ENDEMIC PLANTS

A primary aim of this investigation has been to determine, as far as possible, cause and effect relationships in regard to the strict endemism demonstrated by eight species. Repeated here for convenience, they are: *Aster lowrieanus, Arabis serotina, Clematis albicoma, Clematis viticaulis, Erigonum alleni, Oeonothera argillicola, Solidago harrissii,* and *Trifolium virginicum.*

Mason (1946) has clarified the problem of endemism as follows: "There are three aspects to the dynamics of any problem involving the geographic distribution of plants. First there is the environment, represented by a series of intensity spans of the various environmental factors or by conditions or sequences of conditions of these factors. Secondly there are the physiological reactions of the individual plant that function within limits of tolerance for the conditions prevailing within the environment. Thirdly there are the genetic processes that operate to fix tolerance ranges of and give character to the individual, to control the variability of the population, and to give rise to new individuals preadapted to this environment or endowed with the potentiality for extending the area of the species."

All plant functions are conditioned by the interaction between environmental factors and genetically

determined physiological processes. The physiological and genetical nature of these endemics, then, is a measure of the environmental conditions peculiar to their habitat. Conversely, an understanding of environment is an indication of the physiological tolerance of plants restricted to it. For practical purposes, only those factors which are probably limiting have been critically examined with respect to their interaction on the physiology of the endemics. Also, the assumption is made that these limiting factors are included in factors unique to the barren areas.

NATURE OF ENVIRONMENT

Although environmental conditions have been presented in some detail, it is desirable to emphasize certain factors and conditions thereof which have a pertinent bearing on the problem of endemism. The unique environment is the result not only of combinations of factors, but also of rhythmic sequences of these combinations which vary from point to point in intensity. Factors of substratum, exposure and slope are responsible for an edaphic situation in which the C horizon, adequate for continuous plant growth, is overlain by a layer of rock fragments which becomes drastically less favorable as the growing season progresses. These factors, coordinated with growth processes, are responsible for the sparse vegetational cover with its accompanied reduction in competition.

PHYSIOLOGICAL TOLERANCES

Pertinent physiological processes are discussed in order of occurrence in the life cycle. Data previously given are briefly reviewed. It has been impractical to examine each endemic with respect to each environmental condition studied. Only five have been subjected to laboratory experimentation. Referred to as the five experimental species, they are: *Clematis albicoma, C. viticaulis, Eriogonum alleni, Trifolium virginicum,* and *Oenothera argillicola.*

All of the endemics produce effectively disseminated seed, as evidenced by their distribution. Germination percentages are high for the five experimental species, as observed in the laboratory and in the field. Breaking of the various types of dormancy, as determined in the laboratory for the same species, is adapted to conditions present. The environment, therefore, imposes no critical limitations on these processes. Since such a large proportion of the seedlings on the barrens is of these species, it might appear that they are better adapted with respect to seed germination than many of the other species present.

Seedling establishment is subject to increasingly adverse temperature and moisture conditions of the surface layer, as the growing season progresses. Tolerance limits to surface temperatures, as determined for *Oenothera argillicola*, ranged from 46 to 54° C, with an average of 52° C (Fig. 17). Field observations on the other experimental species demonstrated a similar range. Since, subsequent to seed germination, temperatures over most of the surface greatly exceed this, it constitutes a limiting factor on the number of plants established. On the other hand, this relatively high temperature tolerance enables some seedlings to survive in more favorable parts of the surface layer, and it must be considered an adapation for survival. This severe weeding out also provides for a condition of greatly reduced competition, which is evidently also essential to survival of the species.

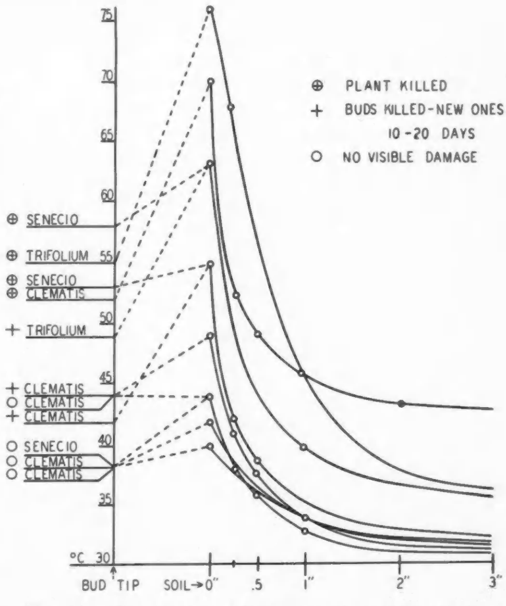

FIG. 17. Temperature effects experimentally obtained on 3 shale barren plants. Temperatures were maintained for one 7-hour period. Although bud tips (0.5-1.0" high) are closer to the heat source, their temperatures lag those of the soil surface by 2-20° C. The soil temperature gradients, only the upper 3 inches of which are plotted, are similar to those which were obtained under natural conditions. Plant organs did not withstand temperatures much in excess of 40° C. The entire plant was killed when the upper soil layer, containing the perrenating organs, was heated in excess of 40° C. Variations in temperature effects are due to the relative position of the organs and to their shading effect on the soil surface immediately below.

The extensive root systems (Fig. 15) of all endemics are obligate upon a relatively deep soil, or a thinner soil if overlying a loosely fractured substratum. The concomitant increase in ability to secure water and nutrients facilitates their survival through adverse summer conditions. The tolerance of the endemics to moisture and nutrient levels in other habitats is not known. Since, however, the five experimental species do well under cultivation, at least these can probably tolerate or even grow better on more favorable soils frequently found adjacent to the barrens.

Perennating organs of all endemics survive adverse conditions throughout the year, their tolerance

being at least equal to the range of climatic factors as previously given. Likewise, these organs can withstand surface temperatures encountered at the time spring growth is initiated. About 60 buds of 25 plants of *Clematis albicoma, Trifolium virginicum,* and *Senecio antennariifolius* (a near endemic with the same habitat preference) were subjected to various levels of radiant energy (Fig. 18), by the method used for determining maximum seedling temperature tolerances. Results show that (1) bud temperatures of 38-58° C lagged 2-20° C behind those attained by the exposed soil surface, and (2) their critical lethal temperature was 42-44° C. Temperatures of 52° C and above resulted in death of the entire plant. That these plants begin rapid growth in early spring, even before seeds germinate, is further possible evidence of their adapation to adverse conditions, as is also their ability to develop new buds whenever existing vegetative growth is destroyed, particularly in Eriogonum and species of Clematis.

Photosynthetic compensation points of all endemics are evidently high. The endemics are rarely observed in shaded areas, even when such areas are outwardly similar in all other respects to the exposed ones. To supplement field observations, the following experiment was initiated on May 11, 1948 and continued for a period of 4 weeks. Three outside areas were selected to provide three different habitats in respect to light intensities: (1) receiving direct insolation throughout most of the day; (2) densely shaded for most of the day, but receiving a little sun in late afternoon; and (3) intermediate in respect to the others, and receiving direct sunlight for about two hours in the morning and unobstructed sky light for the remainder of the day.

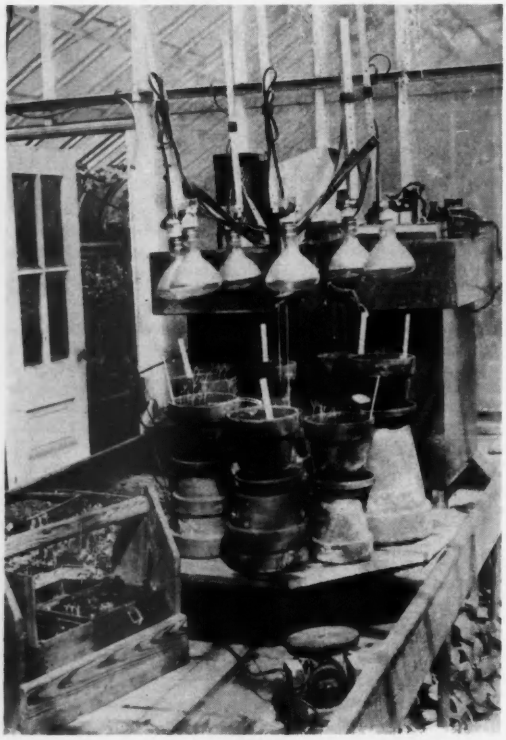

FIG. 18. Device for obtaining experimentally produced temperature effects on plants. Pots, containing pine seedlings, in this instance are rotated at 3 r.p.m. under the infra-red lamps by a constant speed motor. Intensity is controlled by distance from lamps and by variation in voltage.

Forty-five pots containing 136 individual plants were distributed over these locations. These included young seedlings, plants germinated in the greenhouse the previous summer, and mature plants moved from the barrens. Nine pots were of *Oenothera argillicola,* fourteen of *Eriogonum alleni,* six of *Trifolium virginicum,* eleven of *Clematis viticaulis,* and five of *Senecio antennariifolius,* a near endemic.

Differences in other factors resulting from the diverse environments were minimized as follows. A majority of the pots contained shale barren soil, while the others contained series of uniform mixtures prepared in the greenhouse. All pots were sunk into the ground to about 2 cm from their upper rims. Water was added to the surrounding soil as needed to keep the moisture levels approximately equal. Plants were grouped in respect to history and stage of development, with each group being distributed over the locations in matched pairs or triplicates. Where differences in vigor were observed in these matched groups, the healthiest were placed in deep shade, the next in intermediate shade, and the weakest in sunlight.

In all plants placed in the two extreme locations, differences were noticeable within a week and quite pronounced within a month. Those receiving direct sunlight for most of the day grew normally, while those in deep shade had an opposite reaction. In the latter situation Oenothera plants made no growth, lost their leaves, and died in 1-4 weeks. Plants of the other four species grew very little, if at all. Within a month the less vigorous ones were dead, and all others had responded with a typical shade reaction; petioles and non-woody parts spindly and green color fading. Such effects have been observed on the barrens under similar light conditions. Plants subjected to intermediate light intensities remained healthy but produced scanty or no growth. Both field and laboratory observations indicate then, that these endemics are obligate heliophytes.

The factor of competition is foremost among the direct and indirect effects the organisms have upon each other. Its intensity on the barrens, especially with regard to light, water and nutrients, is at a relatively low level. Water and nutrients, usually adequate, must be sharply limiting at certain times and in certain areas, as indicated above. Light, while abundant in exposed areas because of sparse vegetation, becomes sharply limiting elsewhere on the barrens or on adjacent habitats.

Seeds of the endemic plants are certainly dissem-

inated in great numbers in such habitats as old fields, woodlands, roadsides, cultivated areas and river bottoms. Seedlings of Eriogonum, unique in their appearance, have been found in old fields and roadsides in the early spring, while the herbaceous cover is in a similar stage of development. Yet only very rarely are mature individuals found, and then only in open ground. Seedlings of all endemics studied grew slowly and do not produce seed for two or more years. Furthermore, the developing seedlings, and in some cases the mature plants, remain close to the ground, and so are easily shaded by the faster growing species of road-sides and old fields. Thus competition for light is conditioned by growth habit as well as by obligate heliophytism.

Causes of Endemism

Conclusions on causes of endemism are made for the entire group of strict endemics, despite the fact that a full range of data has not been obtained for each species. This procedure is based on (1) support of principal criteria by data on each species, (2) absence of data contrary to conclusions drawn, and (3) conclusions broad enough probably to include species-variations ocurring.

The endemics are well adapted in structure and physiology to shale barren conditions. They are obligate upon (1) high light intensity, (2) an edaphic medium adequate for their extensive root systems, and (3) a low level of competition. They are restricted to the shale barrens because no other habitat in the whole region possesses this unique combination of soil and light conditions which permits them, but does not permit stifling competitors to grow.

Discussion and Implications

Core (1940) gives with a complete bibliography the distribution of the more notable shale barren plants. Numerous stations added during this investigation generally fill in rather than extend his account. *Oenothera argillicola* and *Trifolium virginicum* alone extend over the whole area from south-central Pennsylvania to southwest Virginia; *Solidago harrissii, Aster lowrieanus* and *Arabis serotina* occur in the central section; and the two *Clematis* species and *Eriogonum alleni* are restricted to the southern part.

All demonstrate a very spotty distribution over barrens within their range, as well as over individual barrens. Populations are restricted frequently to a small part of a given barren, even when nearby parts appear in every respect to be similar. Moreover, one or more endemics may be absent from a certain barren but appear on the next one, where still others are lacking. The probable explanation of this spotty distribution is twofold: (1) seed dispersal is often correlated with topography or with prevailing winds on individual barrens, and by chance between barrens, and (2) populations may be decimated or almost so by infrequent severe climatic conditions; new populations arising from few surviving members of old ones.

Considerable genetic variability in several endemic species is demonstrated by investigations now in progress. Harry T. Stinson, Jr. of the Department of Botany of Indiana University, is making a cytological study of *Oenothera argillicola* material sent him. Preliminary studies indicate differences in chromosome configurations between races occurring on the same barrens and on different barrens. The writer is segregating micro-geographic races of *Trifolium virginicum* on the basis of seed color. He is also working with Dr. Ralph O. Erickson of the University of Pennsylvania on a population study of the species of *Clematis* represented on the barrens. The analysis to date of extensive data, especially on flower and leaf characters, demonstrates unusual genetic diversity within and between populations over the whole range.

Wherry (1930) points out in a discussion of the geographical relationships of endemic and near endemic barren plants, that three centers of origin may be represented. Of the endemics, *Eriogonum alleni* is probably derived from Rocky Mountain species, *Trifolium virginicum* from prairie species, and the others from surrounding species.

This evidence permits certain conclusions as to the age of these endemics and, correspondingly, the age of the shale barrens. The fact that the isolating mechanisms are manifestations of genetically fixed physiological amplitudes existing in a unique combination of edaphic and climatic factors is proof enough that these plants evolved in their present habitat. It follows then, that the shale barrens would have to have been in existence for at least as long as the time required for evolutionary development of the endemics on them.

Geologically the barrens, subsequent to exposure of the substratum by erosion, have been subject to but two variables; climate and vegetational cover. It is impossible to know if this substratum supported, during similar climatic cycles in the past, an extinct flora which effected a drastic departure from present conditions. However, it certainly is unlikely that these barrens could support during the last ice advance the existing endemic flora, since the terminal moraine is less than 300 miles from the northernmost barrens. Furthermore, it is highly improbable that, if this same flora had been in existence prior to the ice age, a refugium having similar conditions was available. Even if the barrens supported a highly plastic endemic flora which evolved in step with changing climate, the physiological tolerances of such species during the ice age would differ greatly from those existing today. In all probability, then, at least the six species believed to have surrounding progenitors have evolved since the last ice age. The same is equally evident for the other two, since their progenitors, most likely migrating to this area during the latter or an earlier inter-glacial period, would have been here towards the beginning of the present thermal period.

Present data on these species indicate that their age, size, isolation, and history, *per se,* are not direct

causes of endemism. Rather, these factors bear an indirect relationship and are descriptive of the situation in which the real causes, as given above, operate. This point of view obviates any tendency to hold in common for these species, because of their indicated youthfulness for example, such characteristics as vigor, aggressiveness, and genetic diversity, in apposition to those characteristics which are sometimes applied to old species. On the contrary, evidence already presented clearly indicates a considerable diversity of such characteristics among these species. A cursory dscription of the better understood endemics will further illustrate this point. Of the only two species extending over the whole range, *Oenothera argillicola* has on an average the greatest population density of any endemic, it may rapidly invade newly exposed shale areas, large numbers of seeds are produced whose germination percentage is high when subjected to normal climatic winter conditions, and the consequent possibilities for hybridization between populations potentially increases biotype variability. The other wide-spread species, *Trifolium virginicum*, has in contrast the smallest population density of any endemic, frequently less than a dozen plants inhabiting a barren, and the total number of populations known is only a fraction of those for Oenothera. Its distribution on a single barren is much more restricted. Seed production is relatively less, and germination is dependent upon breaking of the hard seed coat. Thus biotype variability is potentially lower, as possibly indicated by interpopulation differences in seed color. Of the three species restricted to the southern portion of the barrens, *Erigonum alleni* has much the greater population density and frequency, occupies more niches on the barrens, and demonstrates no readily observed morphological variability. In contrast, morphological variability in the two species of *Clematis* is by far the greatest of barren plants.

The principal points made in this discussion are that (1) the endemics have not filled the area available to them; (2) morphological variability is manifest within some; (3) although they have probably evolved since the last ice age their environment is probably much older; (4) despite common isolating mechanisms great genetic diversity exists between species; and (5) the real causes of endemism lie in the interaction between environmental factors and genetically determined physiological processes of the individual and the population.

SUMMARY AND CONCLUSIONS

An ecological study of the mid-Appalachian shale barrens and of the plants endemic to them was made during the years 1946 to 1948.

Positive correlations between shale barren formation and the factors of substratum, slope and exposure were demonstrated. The fissile, highly siliceous, and consequently more weather resistant nature of the substratum is the primary cause for shale barren formation. Stemming from this, under certain conditions of slope and exposure, are all of the other factors which are responsible for these unique plant habitats. Since these substratum characteristics are possessed, with few exceptions, only by large portions of the Brallier Formation, shale barren distribution is for the most part restricted to outcrops of this formation.

Barrens are formed only on slopes, and none have been found on slopes of less than 20 degrees. Generally, the barrenness becomes more pronounced with increase in slope. On moderate ones barrens have been observed only on areas having a southerly exposure. On east and west exposures they have been observed only where stream action has produced steep slopes and bluffs whose steepness compensates in part for the reduced period of insolation.

The derived soils, developed under the warm, temperate rainy climate with no distinct dry season, are 4-12 inches deep and lack a differentiated zone of eluviation. The only significant difference demonstrated in soil horizons between normally vegetated and barren slopes is the substitution of a surface layer of flattened irregularly shaped weather resistant rock fragments of the barren slope for the A and A_0 horizons of the vegetated slope. The pH of barren slopes ranges from 4.5-5.5, and that of vegetated ones from 4.0-5.0. Soil analyses demonstrate a close similarity between them in nutrient content. No evidence has been obtained which would indicate that either gully or sheet erosion is of significance in barren formation.

Temperatures attained on the barrens are critical in plant growth only at the soil surface, where they are often well above the physiological tolerance of most plants, and also constitute an important factor in evaporation rates. Otherwise, temperatures probably have their greatest effect upon the character of the vegetation, rather than upon its relative prevalence. The evaporative power of the air over the barrens and especially at the soil surface during periods of insolation results in a rapid drying of the surface layer of rock fragments and adjacent silt loam of the C horizon after rains. However, the mulching effect of this surface layer is such that moisture loss from the deeper soil layers is greatly restricted and their moisture levels are equal to those obtaining at similar depths in the C horizon of the vegetated slopes.

Influences of fire and man, including lumbering, are negligible, and are of no significance in barren formation.

Of the 97 flowering plants considered characteristic of the barrens, 19 are indicator species, and of these, 8 are strict endemics. The ecology of the mature stages of the vegetation is markedly different from that of the seed and seedling stages.

Five of these characteristic plants are annuals, 21 are trees and shrubs with perennating organs more than 10 inches above ground, 40 are hemi-cryptophytes with perennating organs just above ground but pro-

tected by leaf rosettes, and 33 are geophytes with perennating organs underground. The mature stages of all perennials are well adapted to survival of winter conditions.

An indication of the ability of the mature stages to survive adverse summer conditions has been obtained by the use of "root-shoot ratios," i.e., a visual estimate of the size and extent of the root system with respect to that of the shoot. The 73 geophytes and hemicryptophytes, with root systems much larger than their shoots, are well established in the C horizon. The general adequacy of this horizon for these plants is demonstrated by the rare occurrence of wilting, by their healthy appearance, including no observable nutrient deficiency symptoms, and by the fact that those species which enter the barrens from other areas do so without evident change. A large majority of this group have their principal growth in the first 6-8 weeks of the growing season when moisture levels are higher than in mid-summer. Individual plants are, in general, widely spaced from each other.

The 21 trees and shrubs have root systems which become proportionately smaller and less effective as the growth demands of the shoot increase with age. Growth rate measurements demonstrate a marked stunting of such plants growing on the barrens, in contrast to those growing on adjacent normally vegetated slopes. This stunting is an evident result of low moisture conditions in the surface layers of soil and rock fragments. The C horizon, in which these plants are rooted, is adequate for young stages. However, with increase in size and a corresponding need for increase in the number of surface feeder roots. the moisture and consequently the available nutrients characteristic of the A and leaf mold horizon of the vegetated slopes are not available on the barren slopes. Despite stunting and loss of vigor it is of significance that a negligible percentage of this group die in early maturity.

The 5 annuals, with about 1:1 root-shoot ratios, are shallowly rooted in the C horizon, and are in general restricted to the parts of the barrens where moisture levels are relatively high.

Seed germination studies on representative species indicate that critical quantitative limitations on barren vegetation are not imposed either by the number, distribution, and viability of seed produced or by the climatic conditions requisite to breaking the various kinds of seed dormancy demonstrated. Seeds are largely disseminated on or within the upper portion of the surface layer of rock fragments. Consequently both seed germination and seedling establishment are equally restricted to this region. Although moisture conditions in the early spring permit germination to a limited extent, the extremely adverse moisture and temperature conditions within this layer for the remainder of the growing season almost completely eliminate seedling establishment and are, therefore, the principal reasons for sparsity of plant life on the barrens.

The real causes of endemism are resolved in the interaction between environmental factors and genetically determined physiological processes of the individual and the population. The endemics, in their evolution, have become obligate upon a high light intensity, a soil adequate for their extensive root systems and a low level of competition. They are restricted to the shale barrens because no other habitat in the general region possesses this unique combination of soil and light conditions which permits them, but does not permit stifling competitors to grow.

The fact that these common isolating mechanisms are manifestations of genetically fixed pysiological amplitudes existing in a unique combination of edaphic and climatic factors is proof that these plants evolved in their present habitat. It follows then that the shale barrens would have to have been in existence for at least as long as the time required for speciation of the endemics on them. The time required for this speciation is most likely in terms of ten to twenty thousands of years, since it is highly improbable that this flora could have been supported by the climate of the last ice age. On the other hand the barrens must have been in existence for as long as their substratum has been exposed, unless prior to the present thermal period this was either vegetated by now extinct species, or subjected to climates which brought about a different type of soil formation.

The endemics hold in common these isolating mechanisms and evident youthfulness. Considerable diversity has been demonstrated with respect to probable centers of origin, distribution patterns, population densities, and biotype variability.

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THE ASSOCIATIONS OF BARK-INHABITING BRYOPHYTES IN MICHIGAN

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INTRODUCTION

The relationships between bark-inhabiting bryophytes and the trees upon which they grow must be given much more attention if their position in community structure is to be understood. This investigation was undertaken to determine whether bryophyte communities on bark are correlated with forest climaxes in Michigan or are characteristic of a given region regardless of the tree species (or rocks) upon which they are growing.

Sincere appreciation is expressed to Professor H. H. Bartlett and particularly to Dr. William C. Steere under whose guidance the investigations progressed.

RELATED STUDIES

Cain and Sharp (1938) have given a summary of bryocenological studies that includes the more important works done on the bark-inhabiting bryophytes through 1937. Collections of, and taxonomic studies on, the bryophytes of Michigan have produced some helpful notes on distribution and the tree species upon which they are found.

For the Great Smoky Mountains of Tennessee, Billings and Drew (1938) described ten "unions" based on maps of the bryophytes on four Liriodendron trees, and one each of Aesculus, Castanea, Fagus, and Fraxinus. These bryophyte communities were based on "presence classes." General notes are given in the discussion of the communities concerning the area covered (coverage) by some of the species as drawn on maps of the bryophytes. No unions found on deciduous trees were found on hemlock (*Tsuga canadensis*), a fact explained by its drier and more acid bark. Billings and Drew concluded that bryophyte communities form a zonation on the butts of trees due to differences in bark moisture and that the zones replace each other as the bark matures. An equilibrium is reached when the mesophytic mosses reach a height where desiccating winds counter-balance any improvement in bark moisture due to bark changes.

Also in the Great Smoky Mountains of Tennessee, Cain and Sharp (1938), studying bryophytes in different habitats, used the technique of mapping the bryophytes on tree butts. Of interest in this investigation are their middle trunk communities, (1) a *Frullania asagrayana* "union," and (2) a *Neckera pennata* "union." They give excellent definitions of statistical classes, frequence, presence, and constance. In recognizing "corticolous" communities they utilized coverage and presence.

In northern Italy, Jaeggli (1938) described four "associations" based on investigations with quadrats and a "total estimate," combining density and coverage as used by Braun-Blanquet (1932). He also used a "presence scale" of five degrees, which are expressed in terms such as "constantly present" and "mostly present." He drew idealized sketches showing the differences between isolated trees and forest trees. After investigations of factors, he concluded that rainfall with its resultant humidity is most important for bryophyte development and that light and temperature exert their influence chiefly through their effects on moistures.

In Argyll, Scotland, Martin (1938) drew idealized sketches of the difference between bryophytes on young and old trees and sheltered versus exposed sides based on frequency in a study of two hundred twenty-

seven trees. She used "frequency" in the sense of occurrence of species on different trees.

In Killarney, Ireland, Richards (1938) tabulated the occurrence of bryophytes chiefly on oak trees, and distinguished a climax "associule" on the smaller tree branches and one on the more humid and shadier trunks. These "associules" were based on the "frequency" of species expressed in four symbols: present, present in large quantities, dominant and subdominant.

On Haya Island in Oslo Fjord, Stormer (1938) distinguished two "soziations" of bryophytes on tree trunks, based on the so-called "joint constance" of species. "Joint constance" was based on five quadrats of the community on one tree and five quadrats on other trees containing related "variants" of the typical community. He also presented figures for area covered by each species which he termed "cover degree," and averaged these figures for all the quadrats of a community.

In Indiana, Young (1938) investigated bark factors and concluded that moisture is the most important one for bryophyte development. Wind is also significant because of its drying effect.

At Mountain Lake, Virginia, Patterson (1940) recognized nine well-developed bark-inhabiting "societies" based upon the dominant species found in quadrats on random mature trees which carried well-developed communities of bryophytes between five and seven feet from the soil. He considered dominance to be the same as the area covered by a species, for which he used the term "cover degree." After a study of factors, he concluded that the individual occurrences and distribution of corticolous bryophytes depend on the different levels of evaporational stress and the different moisture-holding capacities of the bark substrata.

In New York State, Brown (1948) studied the distribution of epiphytic plants and concluded that different combinations of factors lead to a number of microclimates and that the important factor of evaporational tension is affected by all of these and the host species upon which the epiphytes grow. She states, however, that no marked selectivity is shown for host species. She also points out the importance of the morphology of epiphytes in their relative success.

In investigation of the ecology of cedar glades (*Juniperus virginiana*) in Tennessee, Quarterman (1949) concludes that the red cedar is more than a mere substrate for corticolous bryophytes; therefore the bark species do not form associations apart from the organism on which they grow. She distinguishes successional stages correlated with age of tree consisting of a pioneer stage (*Frullania-Orthotrichum*) followed by a complex of species including *Leucodon julaceus* and *Cryphaea glomerata,* and then older mats of Leucodon and *Porella platyphylloidea.* This succession is modified by position of the tree outside, at the margin of, or within a stand.

TERMINOLOGY

The diverse use of ecological terms requires a consideration of those used in this study.

The word "community" is used in the most general sense to include all categories of sociological groupings. In general the term "association" will be used in a broadly inclusive sense, applied to various communities differing from one another in the proportion and number of minor species represented and may therefore be made to apply to unmixed communities of a single species as well as to mixed communities. Each community may be considered more or less arbitrarily as belonging to an association or as being intermediate between two associations. The only objection to using the term for bryophytic communities is that it might imply equal rank with associations of higher plants. However, prefixing the name of the bryophyte species indicates clearly the nature of the association.

The "stand" is the particular representative of an association that occurs at a particular spot. On the basis of their make-up there may be an indefinite number of more or less different stands which, however, have certain dominant features in common and therefore are representatives of the same association.

Those community characteristics which are of value in investigating bark-inhabiting bryophytes include coverage, vitality, constancy, and geographic distribution of species within the community range. "Coverage" designates the relative proportion of a community covered by a given species. Subjective "vitality" evaluations are included in the discussion of the various associations. Constancy is the degree of regularity with which a species appears in unit minimal areas of different examples of an association. In investigations of bryophytes on trees, each tree may be considered as a separate stand of the bryophyte community that it contains, so that constancy is considered here to represent the occurrence of a given species on different trees (and tree species) in a given locality (e.g., a beech-maple stand), and can be designated "local constancy." This makes necessary another term to indicate the general distribution of an associated species throughout the bryophyte community range, i.e. in the several to many different localities where single tree stands bear many bryophyte stands. This can be designated as "general constancy" (see Hilitzer, 1927).

General community distribution of associated species is, of necessity, geographically limited because geographic distribution is largely determined by climatic factors. Different species are differently limited by climatic factors, and it is therefore clear that a species may occur in the communities of an association in one place and yet will be entirely lacking elsewhere, even though the specific composition and aspect of the association in a broad sense are little changed.

The communities are recognized, then, on the basis of the coverage, local constancy, vitality, and geo-

graphic distribution or general constancy of the bryophyte species. Those species with the highest coverage, constancy, and vitality were considered dominant and associations have been named after the dominant species.

Those species which have the highest local constancy and occur with the dominant species over the greatest part of its range (general constancy) should be considered together with the dominant, as "characteristic" of the association. "Characteristic" is used here in the sense that the given species would have a high probability of occurring in any sample of the given community investigated.

The terms "associated" and "associates" are used in their normal English sense, to indicate that a species grows with another species.

The nomenclature for bryophytes is taken from Steere's "The Bryophyte Flora of Michigan" (1947).

REGIONS CONSIDERED

This investigation has been made in Michigan, which extends from latitude 41°-45′ to 48°-20′ north and from longitude 82°-25′ to 90°-34′ west. The state is divided into the Upper and the Lower Peninsulas by the Straits of Mackinac (Fig. 1). The Upper Peninsula has Lake Superior to the north, Lake Michigan and Lake Huron to the south, whereas

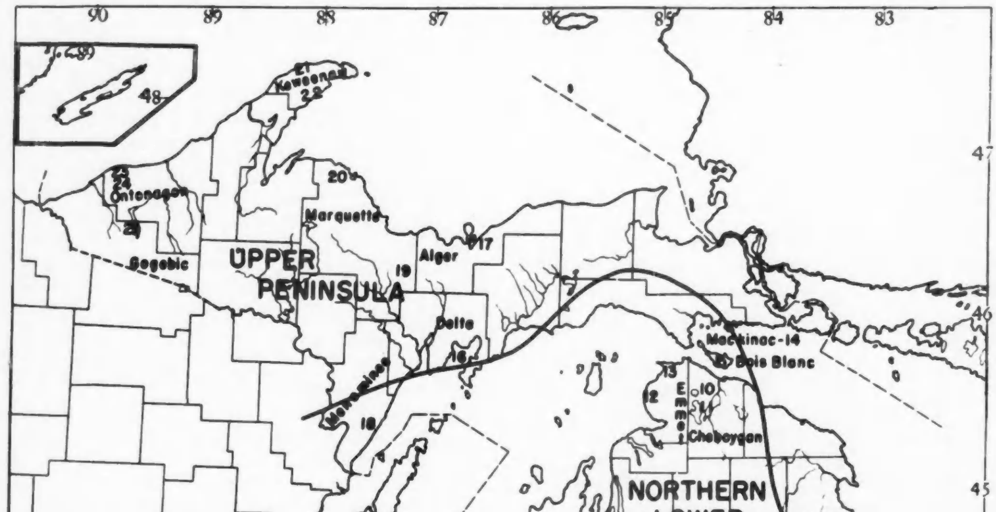

FIG. 1. Divisions of the State of Michigan as recognized in the study, together with general moisture conditions. Localities of study are indicated by name and number.

the Lower Peninsula has Lake Michigan to the west and Lake Huron to the east. The total area of the state is 58,915 square miles, with over 1,600 miles of coastline on the Great Lakes, the longest lakeshore line of any state in the Union. Since the greatest length of the Upper Peninsula is from east to west (318 miles), whereas the greatest length of the Lower Peninsula is from north to south (277 miles), the state as a whole extends over a wider area than might be expected.

The fifty localities investigated in twenty-five areas are listed in Table 1. The main divisions used in this study are the Southern Lower Peninsula, the Northern Lower Peninsula (including the Islands in the Straits of Mackinac), and the Upper Peninsula. These divisions, the counties and the areas of study are indicated in Figure 1.

CLIMATE

The development and distribution of bark-inhabiting bryophytes in Michigan indicate that the two climatic conditions of most importance are temperature and moisture.

The important climatic differences affecting this development and distribution and the separation of Michigan into three regions are clarified by Thornthwaite's (1948) system for the classification of climate which includes the factor of evaporation. He used the term "potential evapo-transpiration" to indicate the combined amount of water that would transpire from plants and evaporate from the soil if the water were available. This amount was determined by a discovered relationship between it and the mean monthly temperature after adjustments were made for the length of day. He was able to draw lines on a map of the United States to indicate regions based on the calculated annual average potential evapotranspiration. Another map indicates the regions of the United States on the basis of a moisture index which is an expression of the amount of surplus water or its deficiency. Figure 1 indicates the lines between the regions in Michigan, as adapted from Thornthwaite's maps (Fig. 3 and Plate Ia, 1948). The figures are summarized as follows:

	Potential Evapotranspiration	*Moisture Index*
Southern Lower Peninsula	24-30 inches	20-40
Northern Lower Peninsula	18-24 inches	20-40
Upper Peninsula	18-24 inches	40-60

With a similar moisture index the southern Lower Peninsula and the northern Lower Peninsula are separated by the potential evapotranspiration which is higher in the south, making the climate drier there. The northern Lower and the Upper Peninsulas have similar potential evapotranspiration but the upper Peninsula is more humid because of its higher moisture index which indicates that more moisture is available there.

METHODS

In this study covering a fairly wide and diverse area, various methods had to be used. Where a single bryophyte species occurs, observation alone is sufficient without quantitative data. Other methods that have been used include: (1) The Quadrat method, which may or may not include the use of devices such as plastic frames; (2) The Mapping technique, in which the actual position and extent of the bryophyte species is charted on grid paper of some type; and (3) The "Entire-stand" technique, in which the entire bryophytic stand of a community on a tree is considered as a unit. Quantitative methods were used extensively and were useful in fixing in mind the association concept. Hundreds of quadrats in many localities where conditions were favorable and all the quadrats available in less favorable habitats were tabulated. Thus these methods were given a thorough trial and none found to give entirely adequate and satisfactory results. As suggested by Cain and Sharp (1938) methods yielding data giving adequate pictures of the community are valuable but the technique of sampling should not be allowed to usurp the more important place. For example, quantitative data might indicate that a certain species was a characteristic species of a given association whereas wider experience, observation and investigations of other associations might reveal that the chosen species was either an invader or a relic of another association.

The whole growth of bryophytes on a tree is advantageously considered as a unit in a region where the tree is not fully covered and where the various communities are distinct. In such instances, a square decimeter is such a large percentage of most stands in Michigan, that it is almost as good a sample as the entire stand. Quadrats have the further advantage of affording some statistical comparisons of stands on different trees. When the tree is covered with bryophytes from the base to a considerable height, any attempt to consider the whole growth as a unit is extremely confusing, since the dominant bryophyte species change up and down the tree and of course on different sides of the trunk.

The same communities were studied in a preliminary analysis using different methods. In one study, ten northern white cedars (*Thuja occidentalis*) of four to six inches DBH were studied in the field by the use of plastic quadrat-frames, one decimeter square. These plastic frames were divided by thin crosswires so that each space was ten per cent of the total. Figures for coverage of each species were noted at 0.5, 2.5, and 4.5 feet heights on the north, south, east, and west sides of the trees. The bryophytes on these same trees were then mapped on graph paper, and figures for coverage recorded from the maps. Map-making proved an arduous task and was not considered to be worth the time and effort involved. A third method was then used in

TABLE 1. Regions of study, tree climaxes, bryophytic associations,* and moisture.**

Regions—Parts County—Locale	Tree Climaxes Remarks	Bryophytic Associations	Moisture
SOUTHERN LOWER PENINSULA			
1. Washtenaw— S E			
A. Waterloo Area	Isolated—roadside	HOp	1
B. Scio	Oak—hickory	HOp	1
C. Saginaw Forest	Populus planting	HOp	1
D. Stinchfield	Isolated fence rows	Op	1
E. Hudson Mill	Isolated roadside	Op	1
2. Wayne— S E			
Plymouth Woods	Edge—beech—maple	H	2
3. Oakland			
A. Green's Woods	Mixed beech—maple Oak—hickory woods	H	1
B. Oakwood Road	Open cedar swamp	H	2
C. Bass Lake	Marl lakeshore	HOp	2
4. Lapeer— S E			
Imlay City	Cedar bog	F H Py	3
5. Berien— S W			
Warren's Woods	Stream banks in Beech—maple woods	A H	3
6. Cass— S W	Beech—maple plus oaks		
Russ Woods	....	H	2
NORTHERN LOWER PENINSULA			
7. Manistee— W			
Little M. River	Cedar along stream	F H	2
8. Missaukee— W			
Lake City	Cedar swamp	FHLPtR	4
9. Alcona— E			
A. Cedar Lake	Cedar swamp	F Py	4
B. Hubbard Lake	Cedar swamp	F Py	4
10. Cheboygan— Cen			
N. Shore Burt Lake			
A. Hermit's	Mature cedar bog	FHLNPoPyRUPt	4
B. Gorge	Mature cedar bog	FHLNPoPyRUPt	
C. Reese's Bog	Mature cedar bog	FHLNPoPyRUPt	4
11. Cheboygan— Cen			
A. Mudlake	Cedar—lakeshore	H	3
B. Colonial Point	Beech—maple woods	H Py	3
12. Emmet— W			
Cross Village			
A. Lake Bank	Cedar—sandy bank	F Py	2
B. Roadside	Isolated	ALPoPtPy	3
13. Emmet— W			
A. Wilderness	Cedar bogs along	Py	
B. Cecil Bay	Lake Michigan	F H Py	2
STRAITS OF MACKINAC			
14. Mackinac			
Mackinac Island			
A. Bare limestone	Cedar	FLNPy	3
B. Beech—maple	Beech—maple woods	FHLNPoPtPyU	
15. Mackinac			
Bois Blanc	Cedar bogs	HLNPtPyU	3
UPPER PENINSULA			
16. Delta— S. Cen			
Burnt Bluff			
A. Limestone Cliff	Isolated cedar	H	1
B. Woods Cliff Top	....	F	2
17. Alger— N. Cen			
A. Pictured Rocks	Beech—maple, cedar cliffs	FHLN	3
B. Miner's Falls	Beech—maple, cedar ravine	AFLNOsPoPy	5
C. Munising	Cedar bog—water works	FPyR	2
18. Menominee— S. Cen			
Cedar River	Beech—maple plus cedar	FN	3
19. Marquette— Cen			
Dukes National Forest	Maple woods	FL	2
20. Marquette— Cen			
Huron Mountains	Beech—maple woods	N	3
21. Keweenaw N			
Lakes—Streams			
A. Eagle Harbor	Cedar	F	1
B. L. Fanny Hooe	Cedar	F	2
C. Fanny Hooe Creek	Cedar	F	2
D. Lake Labelle	Cedar	N	2
22. Keweenaw— N			
Mountain Woods	Beech—maple woods		
A. Keweenaw Park	....	FPy	3
B. Mountain Road	....	FLNOs	2
C. Mt. Horace Greeley	....	LPy	4
D. Mt. Bohemia	....	F	3
E. Cliff View Drive	....	L	3
23. Ontonogon— W			
Porcupine Mts.	Maple woods		
A. Lake of Clouds	....	LNPo	4
B. Mirror Lake Trail	....	ANOs	4
24. Ontonogon— W	Maple woods		
Porcupine Mts.			
A. Mirror Lake Trail	....	LN	5
B. Nonesuch Mine	....	N	5
25. Gogebic— W	Open Lakeshore State Park		
Gogebic Lake		N	4

*MOISTURE CONDITIONS
1—Very dry
2—Dry
3—Moist
4—Wet
5—Very wet

**ABBREVIATIONS FOR BRYOPHYTIC ASSOCIATIONS
A—*Anomodon minor*
F—*Frullania eboracensis*
H—*Homomallium adnatum*
L—*Leucodon sciuroides*
N—*Neckera pennata*
Op—*Orthotrichum pumilum*
Os—*Orthotrichum sordidum*
Po—*Porella platyphylloidea*
Pt—*Ptilidium pulcherrimum*
Py—*Pylaisia selwynii*
R—*Radula complanata*
U—*Ulota crispa*

which bark quadrats, one decimeter square, were cut from the trees and brought into the laboratory for analysis under a binocular widefield dissecting microscope. As expected, the three methods gave similar statistical results. The third method, which may be called the "Lab-quadrat" method, permitted, in addition, a study of the micro-relationships of bryophyte species, as growth habits, competition, successions, tension zones, invasions and secondary invasions. The Lab-quadrat method consumes less time in the field and permits investigation of a much wider variety of habitats, particularly on long trips with other botanists when materials must be obtained rapidly but with sufficient notes for a careful laboratory study later.

Notes taken in the field include location of stands, forest type (or isolated trees), habitat, shelter, tree species, tree diameter, exposure (side of tree from which quadrats are taken), and a preliminary analysis of the species of bryophytes present, their comparative coverages and vitality.

Table 1 summarizes the bryophyte associations, regions, tree climaxes where found, and an estimate of moisture conditions. Table 2 lists the bryophyte species that occurred in this investigation and the tree

TABLE 2. Bryophytes on trees investigated in various regions.

Key
S Southern Lower Peninsula
N Northern Lower Peninsula plus Islands
U Upper Peninsula
A All Regions

	Abies balsamea	*Acer saccharum*	*Amelanchier canadensis*	*Betula lutea*	*Betula papyrifera*	*Carya ovata*	*Cornus florida*	*Fagus grandifolia*	*Fraxinus nigra*	*Juglans nigra*	*Larix laricina*	*Ostrya virginiana*	*Platanus occidentalis*	*Picea mariana*	*Pinus strobus*	*Populus deltoides*	*Populus tremuloides*	*Quercus alba*	*Quercus borealis*	*Taxus canadensis*	*Thuja occidentalis*	*Tilia americana*	*Tsuga canadensis*	*Ulmus americana*	Number of Tree Species
Amblystegium serpens																		S							1
Anomodon attentuatus		U																							1
Anomodon minor		A						U	A			NU						S			NU	NU			7
Bryum capillare																S		S						S	3
Ceratodon purpureus																S								S	2
Cololejeunea biddlecomiae									N													U			2
Drepenocladus uncinatus		U															N				NU				3
Encalypta streptocarpa																								S	1
Frullania asagrayana	N																				N		N		3
Frullania bolanderi	U	NU		U				NU											N		NU		U		7
Frullania eboracensis	A	A	N	NU	NU	S	S	NU	A		N	NU	S	N		S	NU	SN	U		A	A	NU	SN	21
Frullania selwynii																					N				1
Haplohymenium triste		U																			S			N	3
Homomallium adnatum	S	A		NU	N	S		N	SN	S			S			S	N	SN			N	S	NU	S	16
Hypnum reptile				N																	NU				2
Lejuenea cavifolia																					N				1
Leskeella nervosa		N										N									N				3
Leucodon sciuroides	U	NU		U	U			N	NU			NU							U		NU	NU	NU	N	12
Lindbergia austinii							S									S		S			NU	S		S	6
Lophocolea heterophylla																		S				N		S	3
Mnium ciliare																					N				1
Mnium cuspidatum																S									1
Neckera pennata		NU		NU	U			U	NU			NU					N				NU	NU	U	N	11
Orthodicranum montanum	N	S		NU	N										N			S			SN		NU	N	9
Dicranum viride		U		NU	N				N						N						NU		U	N	8
Orthotrichum elegans		NU		U	U							N					NU				NU	NU			7
Orthotrichum obtusifolium		N		N				N				N				S	NU				SN	N	N	SN	10
Orthotrichum pumilum		SN					S	U		S		N				S		S			S	SN		SN	10
Orthotrichum sordidum	U	NU		U	U			NU	N			U		N			U		U		A	NU	U	N	14
Porella platyphylloidea	N	NU		NU				NU	NU			NU					N				NU	NU		N	10
Ptilidium pulcherrimum	N	N		N	N							N			N		N				N		NU		9
Pylaisia selwynii	N	NU		NU	NU			NU	NU		N	NU		N			U	S			NU	NU	NU	SN	15
Radula complanata		U		U				U	A			U					N	S		N	A	N	N	SN	12
Thuidium recognitum										S											SU			S	3
Tortella tortuosa																								S	1
Tortula papillosa										S						S					S			S	4
Ulota crispa	N	NU	N	NU	N			NU	N		N			N			N			N	NU	N	NU	N	15
Ulota ludwigii								N																	1
Number of Bryo. spp.	11	21	2	16	11	2	3	14	12	4	3	13	2	4	3	9	12	11	4	2	28	16	14	22	

species upon which each was found in the three regions. These tables may be consulted during the reading of the succeeding section on the bryophyte associations.

THE BRYOPHYTE ASSOCIATIONS

HOMOMALLIUM ADNATUM ASSOCIATION

Predominantly in the southern Lower Peninsula, *Homomallium adnatum* forms an association on isolated trees or in open woods, where conditions are generally dry. Here it occurs mostly on deciduous trees and on northern white cedar and may be considered the most characteristic bryophyte community on older parts of trees of the region. Farther north, this association appears in drier habitats, particularly on conifers and the harder-barked deciduous trees, as beech (*Fagus grandifolia*). While more common in the southern Lower Peninsula, this association occurs in twenty-two localities of the fifty localities investigated, and in all three regions.

Frullania eboracensis (occurring in 15 localities in the three regions), *Orthodicranum montanum* (in 7 localities in the northern two regions), and *Lindbergia austinii* (in 2 localities, one in the southern Lower Peninsula and one in the Upper Peninsula) are species which are found often enough (with high local constancy) or over a wide enough area (with high general constancy) to be considered characteristic species. Although other species sometimes occur, they are not characteristic of this association. *Orthotrichum pumilum, O. obtusifolium,* and *Tortula papillosa* occurred in some stands in the southern Lower Peninsula, but as independent units of small

coverage, whereas *Ceratodon purpureus* and *Bryum capillare* are ubiquitous mosses accidentally growing on this habitat. *Anomodon minor* is an invader from the tree base and was found in one locality, Russ Woods. In the northern Lower Peninsula, invaders from other associations are *Radula complanata, Ptilidium pulcherrimum, Porella platyphylloidea, Ulota crispa, Lophocolea heterophylla, Leucodon sciuroides, Orthotrichum sordidum,* and *Dicranum viride.* The very low coverage of the other species indicated the complete dominance of Homomallium.

Communities of other regions similar to this association are: (1) In Indiana, Wilson's association (1936) of *Homomallium adnatum* in a federation of *Homomallion adnatum;* and (2) on Long Island, New York, Cain and Penfound's (1938) union of *Homomallium,* which includes *Frullania eboracensis, Dicranum montanum (Orthodicranum montanum), Ptilidium pulcherrimum, Frullania asagrayana,* and *Lophocolea heterophylla.*

FRULLANIA EBORACENSIS ASSOCIATION

Frullania eboracensis forms an association chiefly of the northern Lower Peninsula, Islands and Upper Peninsula, and was found only once in the southern Lower Peninsula in a northern white cedar swamp near Imlay City, Lapeer County. Elsewhere in the south, this hepatic, occurring in 23 localities in all three regions, is characteristic of the *Homomallium adnatum* association. *Frullania eboracensis* usually produces a pure association as in hundreds of stands that were investigated during studies on the effect of light on bryophyte development and distribution, in which it was the only species present. Frullania is not restricted to this one community but occurs also in many other associations.

Characteristic species of this association where it is not in pure stands are *Radula complanata* (in 9 localities in the northern two regions), *Orthotrichum sordidum* (in three localities in same regions), and on conifers, *Ptilidium pulcherrimum* (in 2 localities in 3 regions). Species of other associations occurred in some of the stands indicating the probable succession in those particular stands, as *Homomallium adnatum, Pylaisia selwynii, Neckera pennata,* and *Leucodon sciuroides. Ulota crispa* occurred in the stands only as independent, isloated units. *Porella platyphylloidea, Anomodon minor,* and *Orthotrichum obtusifolium* were found only in Menominee County, Upper Peninsula, on a damp northern white cedar where the Frullania was not as dominant as usual. *Leskeella nervosa* was associated with Frullania only on Mackinac Island as an invader from the tree base, and here the two species were interwoven strand by strand. *Orthotrichum elegans* is an accidental intruder found only once at the University of Michigan Biological Station, northern Lower Peninsula. Some pure stands of *Frullania bolanderi* form a similar association that seems closely similar in habitat and requirements.

Communities similar to the *Frullania eboracensis* association in Michigan are: (1) on an island in Oslo Fjord, Stormer's *Radula-Frullania dilatata* "soziation" (1938) with species similar to Michigan species, as *Porella platyphylla, Leucodon sciuroides,* and *Ptilidium pulcherrimum;* (2) on Abruka Island in Finland, Lippmaa's *Radula-Frullania dilatata* community (1935) on leafy trees; (3) on Long Island, New York, Conard's *Frullania* "epixylia" (1935); (4) in the Great Smoky Mountains of Tennessee, Cain and Sharp's *Frullania asagrayana* union (1938); (5) in Virginia, Patterson's *Frullania eboracensis* society (1940) which consisted of *Drummondia clavellata, Ulota crispa, Platygyrium repens, Leucodon brachypus* and *Porella platyphylloidea;* and (6) in Ireland, Richard's *Frullania-Ulota* "associule" (1938) on the smaller branches.

LEUCODON SCIUROIDES ASSOCIATION

This association occurs in the northern Lower Peninsula, Islands, and Upper Peninsula, on the deciduous species, sugar maple *(Acer saccharum),* basswood *(Tilia americanà)* black ash *(Fraxinus nigra),* hop hornbeam *(Ostrya virginiana),* and red oak *(Quercus borealis),* as well as on the coniferous species, northern white cedar and hemlock in sixteen localities. In general, this association occurs on trees of smaller diameter than the Neckera association, since it can tolerate somewhat drier conditions. The Leucodon association is found usually on the north and west sides of the trees. However, in extremely moist habitats in the northern Lower Peninsula, as on black ash trees along the stream banks in "the Gorge," and on the maples along the road near Cross Village, shaded and sheltered by dense woods on both sides, Leucodon occurs on the south sides of many trees on which Neckera is found on the moister north and west sides. The Leucodon association occurs with other associations, especially those of Neckera and Porella, and forms many mixed associations with these species.

Although they form their own associations, the following species also have a high local constancy in this association and occur widely: *Frullania eboracensis* (in 12 localities), *Neckera pennata* (8 localities), and *Porella platyphylloidea* (8 localities). *Radula complanata* (6 localities), *Orthotrichum sordidum* (7 localities), and *Pylaisia selwynii* (5 localities) are also characteristic species because of their occurrence and distribution. *Anomodon minor* occurs in the northern Lower Peninsula and in the Upper Peninsula in the moister habitats. *Drepanocladus uncinatus* was found on the Islands and the Upper Peninsula also in wet places. Other species occurring in this association in the northern Lower Peninsula are: *Orthotrichum elegans, Ulota crispa, Leskeella nervosa, Cololejeunea biddlecomiae* and *Orthotrichum obtusifolium. Orthodicranum montanum* and *Anomodon attentuatus* occur in this association only in the Upper Peninsula.

The Leucodon association is circumboreal in distribution. Communities in other regions that are sim-

ilar to the *Leucodon sciuroides* association in Michigan are: (1) Near Oslo, Stormer's "soziation" (1938) of *Leucodon sciuroides*, with its associated species of *Porella platyphylla, Radula complanata*, and *Metzgeria furcata;* (2) Ochsner's association (1928) and Jaeggli's association (1938), *Syntrichietum leucodontosum*, in Switzerland and Northern Italy respectively; (3) In Poland, Wisniewski's association (1929) of *Anomodon viticulosus* and *Leucodon sciuroides* which contained the Michigan species, *Radula complanata, Anomodon attentuatus*, and *Dicranum viride;* (4) In the Rhone Valley, Gam's association of *Leucodon sciuroides* (1928) on "leafy" trees; (5) In Virginia, Patterson's "society" (1940) of *Leucodon brachypus*, associated with *Frullania eboracensis*, Pylaisia, *Anomodon tristis (Haplohymenium triste), Porella platyphylloidea, Platygerium repens* (usually on tree bases in Michigan), *Ulota crispa, Orthodicranum montanum, Frullania asagrayana*, and *Radula complanata*, all of which occur in Michigan; and (6) Gams' *Leucodontetum sciuroidis* (1932), which is part of a federation named *Leucodontion*, widely distributed in Europe.

Pylaisia Selwynii Association

This association occurs in the northern Lower Peninsula, Islands, and the Upper Peninsula, with one southern extension into a northern white cedar swamp in Lapeer County, where it appeared on the soft-barked American elms. The Pylaisia association is found on both deciduous trees and conifers, and its occurrence on younger trees gives some indication that it is a transitional stage, in the sixteen localities where found.

With a good coverage and vitality, Plyaisia completely dominates this association. Even though some of the other species heave a high local constancy, they have a low coverage. Chief species associated with Pylaisia are *Frullania eboracensis* (14 localities), *Neckera pennata* (8 localities), *Leudocon sciuroides* (in 7 localities), *Orthotrichum sordidum* (7 localities), *O. obtusifolium* (5 localities), *Radula complanata* (8 localities), and *Ulota crispa* (5 localities).

Frullania, with its high local and general constancy, is a relic of a previous pioneer community, as is Radula. Since Neckera has the next highest general constancy, the usual succession is to that association. Some of the stands might evolve into associations of Leucodon or Porella or perhaps into mixed associations of Neckera, Leucodon and Porella, since *Porella platyphylloidea* occurs in them. Species of *Orthotricha* and *Ulota* occur as relics in the stands, where they usually pioneered on projections of some kind. *Drepanocladus uncinatus* and *Leskeella nervosa*, usually characteristic of tree bases in wet places, occur in the stands only on the island.

Orthodicranum montanum and *Dicranum viride* occur only on northern white cedar in this association, whereas in the Neckera association these species are found on sugar maple, yellow birch *(Betula lutea)*, and American elm as well. This preference of Dicranum for northern white cedar in the Pylaisia association habitat, indicates that this habitat is not an optimum one, and that the Pylaisia association is an intermediate successional stage. *Leskeella nervosa* and *Drepanocladus uncinatus* are associates on the Islands and *Ptilidium pulcherrimum, Anomodon minor* and *Hypnum reptile* in the northern Lower Peninsula.

Communities of other regions which resemble the association of Pylaisia in Michigan are: (1) in Virginia, Patterson's "society" (1940) of *Pylaisia selwynii*, and other species as *Frullania eboracensis, Leucodon brachypus* (similar to *L. sciuroides*), *Porella platyphylloidea*, and *Platygerium repens;* (2) in Finland, Kujala's "Main Group" (1926) of *Pylaisia polyantha*, with *Orthotrichum speciosum* and *O. obtusifolium;* and (3) in the Rhone Valley, Gams' *Pylaisietum* (1927) with several species of *Orthotrichum* including *Orthotrichum obtusifolium*. Evidently Orthotrichum plays a more important role in some of these European bark-inhabiting communities than in Michigan.

Neckera Pennata Association

The Neckera association occurs in the northern Lower Peninsula, the Islands, and the Upper Peninsula, and is the best developed single association in Michigan. It may be considered the most vigorous bark-inhabiting bryophyte community of greatest bark coverage in these regions, just as the Homomallium association is characteristic of the southern Lower Peninsula. The Neckera association occurs on the north and west side of deciduous trees and conifers of a wide range of diameters in seventeen localities. Its occurrence is more dependent on moisture relations than on tree age. Other characteristic species of the association are *Frullania eboracensis* (15 localities), *Porella platyphylloidea* (14 localities), *Radula complanata* (13 localities), *Leucodon sciuroides* (13 localities), *Pylaisia selwynii* (10 localities), and *Orthotrichum sordidum* (7 localities). Species characteristic elsewhere and occurring, but less characteristic in Michigan, are *Anomodon minor, Ulota crispa, Orthotrichum pumilum, Dicranum viride*, and *Orthodicranum montanum*.

In most bryophyte associations in Michigan, Frullania has a high local and general constancy but low coverage and vitality. In Michigan, Frullania exists as a few strands left over from previous communities, although at times it comes in as a secondary invader on Neckera. The other important species, occur in various amounts in the different stands and form associations of their own, where one or the other is locally more dominant than the Neckera. In the great majority of the stands in the Upper Peninsula, the Neckera association is predominant, with the exception of the drier sites, where hundreds of stands on northern white cedar contained *Frullania eboracensis* only. *Homomallium adnatum* is a relic from a former community and *Drepanocladus uncinatus* occurs only in the wettest sites where the

association occurs. *Haplohymenium triste,* although of importance in the Neckera association in other regions, occurs very infrequently in Michigan, where it and *Anomodon minor* are more characteristic of the tree bases. The species of *Orthotrichum* including *O. pumilum* are found in this association on deciduous trees as well as on conifers, emphasizing again the fact that, under optimum moisture conditions, the preference shown by a bryophyte species for a particular tree disappears. Also, *Ptilidium pulcherrimum,* usually found on balsam fir *(Abies balsamea),* occurs in this bryophyte association on trembling aspen *(Populus tremuloides). Cololejeunea biddlecomiae* was found in this association on basswood in one locality in the Upper Peninsula.

Communities of other regions which correspond to this association of *Neckera pennata* in Michigan are: (1) in the Great Smoky Mountains of Tennessee, Cain and Sharp's *Neckera pennata* "union" (1938), with similar species of *Anomodon tristis (Haplohymenium triste), Porella platyphylloidea, Homomallium adnatum,* and *Orthotrichum pumilum,* which they placed in a *Neckera-Ulota* alliance of unions; (2) in the same region, Billings and Drew's *Neckera pennata* "union" (1938) with *Radula complanata,* and *Anomodon attentuatus* among other species; (3) in Europe, Gaume's Association (1944) of *Neckera pumila* and *Orthotrichum lyellii,* which contains *Ulota crispa* and *Radula complanata* of the Michigan species; (4) in France, Allorge's association (1921) of *Ulota crispa* and *Orthotrichum lyellii* with some species of *Neckera;* and (5) in the Rhone Valley, Gams' *Neckeraceae-Anomodonteta* (1927). Due to the comparatively drier sites in Michigan, the species of *Anomodon* do not reach the importance in this community they do elsewhere. However, when moisture relations are optimum, an association of *Anomodon minor* may be recognized, as well as a mixed association of Neckera and Anomodon in one stand. The association of *Neckera pennata* in Michigan would be placed by Gams (1932) in his federation of *Anomodonto-Neckerion.*

ANOMODON MINOR ASSOCIATION

This association was found on the deciduous trees only, sugar maple, black ash, and hop hornbeam. The trunk diameters of trees upon which stands were located range from 5 to 31 inches, indicating that the species of tree and habitat is more important here than age of tree. This association was found on the moist north side of the trees, probably because of its greater water requirements. It is more characteristic of tree bases throughout Michigan but in habitats of optimum moisture, as at Miner's Falls in the Upper Peninsula, it is found on the trunks. Although comparatively rare (only 4 localities), it is more widely distributed in Michigan than most other associations. It occurs not only in the Upper Peninsula, and northern Lower Peninsula, but in the southern Lower Peninsula as well, in a deep, mature beech-maple woods along a stream bank at Warren's Woods, Berrien County.

Species associated with *Anomodon minor* are *Leucodon sciuroides, Porella platyphylloidea, Pylaisia selwynii, Neckera pennata, Frullania eboracensis,* and *Homomallium adnatum.* The associated species demonstrate that this association invades other associations from the tree base. It forms its own association on the trunk only in the wetter sites.

Communities of other regions which are similar to the Anomodon association in Michigan are: (1) in Indiana, Wilson's (1936) association of Anomodetum, which she placed in a federation of *Homomallion adnatum* (although in Michigan, the association of Anomodon occurs more often with the climax association, *Neckera pennata* in northern Michigan, than with the Homomallium association of southern Michigan in drier habitats); (2) in Virginia, Patterson's "society" (1940) of *Anomodon attentuatus* with *Neckera pennata, Porella platyphylloidea, Leucodon brachypus* (similar to *L. sciuroides*), *Frullania eboracensis, and Amblystegiella adnata (Homomallium adnatum),* among other species; (3) in the Great Smoky Mountains of Tennessee, Billings and Drew's "union" (1938) of *Anomodon attentuatus;* (4) in Europe, Gams' *Neckeraceae-Anomodontetum* (1927). *(Neckera pennata* occurs in the Anomodon association in Michigan as does *Anomodon minor* in the Neckera association); and (5) in Poland, Wisniewski's association (1929) of *Anomodon viticulosus* and *Leucodon sciuroides,* (probably more similar to the Michigan association, since *Leucodon sciuroides* has the next highest constancy in our Anomodon association). As discussed in the section on Neckera, Gams (1932) would include this association in a "federation" of *Anomodonto-Neckerion,* which occurs on neutral or slightly alkaline rocks and tree trunks.

PORELLA PLATYPHYLLOIDEA ASSOCIATION

This association occurs on conifers and deciduous trees, but is more characteristic of the softer barked trees as hop hornbeam, particularly in the Porcupine Mountains, western Upper Peninsula, where it was particularly noticeable on the younger trees. In general, this association occurs on trees of smaller diameter than either the Neckera or Leucodon associations, which is indicative of its pioneer nature. As in most other associations, exposure depends mainly on the habitat, but this association usually occurs on the north or west sides of the trees. Occasionally it was found on the south or west, because of unusal moisture conditions as at the Hermit's, near the University of Michigan Biological Station, northern Lower Peninsula, where many of the black ash trees in an extremely moist, boggy, habitat, are covered on all sides with bryophytes. Here, Neckera and Leucodon occur on the north and west sides and Porella on the south. The occurrence of Porella in relatively drier places indicates the somewhat more xerophytic and pioneer nature of the Porella association.

In the northern Lower Peninsula, Islands and the Upper Peninsula, this association was found sparingly (only 6 localities), and the species associated with it indicate that it competes strongly with other associations. Species associated with *Porella platyphylloidea* include *Frullania eboracensis, Pylaisia selwynii, Orthotrichum sordidum, Neckera pennata, Leucodon sciuroides,* and *Radula complanata.* Porella is a pioneer on the tree trunk, often appearing soon after Frullania or Radula and persists as a relic in other communities as Pylaisia, Neckera, Leucodon. In many of the "closed" associations, it grows on mosses, particularly on Neckera. *Dicranum viride* appeared on black ash in a cedar bog in the northern Lower Peninsula, and *Ulota crispa* on beech on the Islands.

A community similar to this Porella association of Michigan is Patterson's "society" (1940) of *Porella platyphylloidea,* with *Frullania eboracensis,* and *Leucodon brachypus* in Virginia. As already indicated in the discussion of the Leucodon and Neckera associations, these three associations are often mixed and this triple mixture represents the best community development in Michigan.

Radula Complanata Association

This rather rare association (only 4 localities) occurs on conifers and deciduous trees, generally on the north and west sides in the northern Lower Peninsula and the Upper Peninsula. Although the association is rare, Radula, itself, is common in many other associations, particularly in the Frullania association. The Radula association is more common on younger trees and horizontal branches and was the only association found on yew *(Taxus canadensis),* where it covered the one inch stems on all sides.

Species associated with Radula are *Frullania eboracensis, Neckera pennata, Ulota crispa, Leucodon sciuroides, Orthotrichum pumilum,* and *Drepanocladus uncinatus.* As indicated by its occurrence on the younger trees, this is a pioneer association, replaced in optimum habitats by other associations in which Radula-like Porella often grows on and over mosses, particularly on Neckera. A study of the other species in this association indicates that the Radula association will be replaced by Neckera or Leucodon in most of the stands, as the bark becomes older and moister.

A community similar to this association in Michigan is Stormer's "soziation" (1938) of *Radula-Frullania dilatata,* with *Leucodon sciuroides* and *Drepanocladus uncinatus,* near Oslo.

Ulota Crispa Association

This association occurs on conifers and deciduous trees on the north and west sides. Although this species is generally considered to prefer conifers, the association is more common in Michigan on deciduous trees. In general, it occurs on trees of small diameter (3-8 inches). On Mackinac Island, however, it was found only on the larger trees of the harder-barked beech, whereas the younger trees had no bryophytes on them. This association is very infrequent in Michigan (4 localities), on the Islands, and in the northern Lower Peninsula, although the species, itself, occurs commonly in many other associations.

Other species associated with *Ulota crispa* are *Homomallium adnatum, Frullania eboracensis,* and *Ptilidium pulcherrimum,* which indicate the pioneer nature of this association. *Ulota crispa* appears in many of the other associations, usually as separate patches or tufts, in pure stands. The pleurocarpous mosses overgrow the Ulota when conditions are right for them, but Ulota, like Orthotrichum, persists as a relic in closed associations.

Communities of other regions similar to the *Ulota crispa* association in Michigan are: (1) in Europe, Gams' "federation" (1932) of *Ulotion,* composed of the most hygrophilous "societies" as *Ulotetum crispae;* (2) in Switzerland, Ochsner's *Ulotetum crispae,* (1928) with other species of *Ulota* and some of *Orthotrichum;* (3) in France, Allorge's association (1921-22) of *Ulota crispa* and *Orthotrichum lyellii* with *Radula complanata, Frullania dilatata, Orthotrichum* spp., *Neckera* spp., and *Leucodon sciuroides,* among others; (4) in Killarney, Ireland, Richard's "associule" (1938) of *Ulota-Frullania,* on the smaller branches; (5) in Tennessee, Cain and Sharp's "union" (1938) of Ulota on the top limbs of trees; (6) in Virginia, Patterson's "society" (1940) of *Ulota crispa* with *Frullania eboracensis, F. asagrayana,* and *Homomallium adnatum,* among others; and (7) in Tennessee, Billings and Drew's "union" (1938) of *Ulota crispa* on Tsuga butts.

Ptilidium Pulcherrimum Association

This association was usually found on the more acid bark of the north and west sides of conifers or birch, although the species itself grows on deciduous trees as well. However, under windier, drier conditions it sometimes occurs on deciduous trees (hop hornbeam on Mackinac Island). The range of tree diameters on which it occurs is wide and depends somewhat on tree species. It was the only association appearing on white pine *(Pinus strobus)* with either *Orthodicranum montanum* or *O. viride* and only on the larger pines as would be expected.

This is a pioneer association found in the northern Lower Peninsula and on the Islands (6 localities) dominated by *Ptilidium pulcherrimum.* Species associated with it are *Orthodicranum montanum, Dicranum viride, Ulota crispa, Pylaisia selwynii, Drepanocladus uncinatus, Frullania eboracensis* and *Porella platyphylloidea.* On many trees this is long persistant and not generally replaced by other communities, due to the limited moisture. But the persistance of Ptilidium in the Homomallium, Neckera, Pylaisia and the Ulota associations, indicates that succession may occur.

Communities of other regions similar to the *Ptilidium pulcherrimum* association in Michigan are: (1) in Finland, Kujala's group (1926) of *Ptilidium pul-*

cherrimum and *P. ciliare* on pine, spruce and birch; and (2) near Oslo, Stormer's "soziation" (1938) of *Ptilidium pulcherrimum* on birch, with *Orthodicranum montanum* among other species.

ORTHOTRICHUM PUMILUM ASSOCIATION

This association occurs on ilsolated deciduous roadside trees in six localities in the southern Lower Peninsula usually in the bark fissures of old trees (23-30 inches DHB). At Saginaw Forest, near Ann Arbor, the softer-barked cottonwoods *(Populus deltoides)* support several different associations in addition to this one, since the area was at one time dense and protected from drying winds. The establishment of bryophytes on trees younger than usual in the southern Lower Peninsula was thus made possible. This is the only association in Michigan generally characteristic of the east and northeast sides of the trees, indicative of its xerophytic nature and the considerable variation in the micro-climate of the cracks and fissures of old bark. The *Homomallium adnatum* association occurs on the west and north sides of these same trees.

Orthotrichum pumilum dominates the association with *Homomallium adnatum*, a very common associate, indicating that the association is a pioneer one which will be succeeded by the Homomallium association provided that moisture conditions improve. *Orthotrichum obtusifolium* is characteristic of this association and in one stand was a co-dominant. Other species associated with *Orthotrichum pumilum* are *Lindbergia brachyptera*, *Tortula papillosa* and *Frullania eboracensis*. *Ceratodon purpureus* is an accidental invader in this association.

ORTHOTRICHUM SORDIDUM ASSOCIATION

This association occurs on very small deciduous trees (3-6 inches DBH), generally on the north and west sides of the trees. The species persists as a relic in many other associations. As an association, it was found only in the Upper Peninsula, and then very rarely in three localities. Its pioneer nature and close proximity to the Frullania association is indicated by the wide spread occurrence of Frullania in this association. Other associates are *Orthotrichum obtusifolium*, *O. elegans*, *Pylaisia selwynii*, *Leucodon sciuroides*, *Porella platyphylloidea*, and *Ulota crispa*, some of which indicate an eventual succession in the various stands where found.

Communities of other regions which are similar to these Orthotrichum associations in Michigan are: (1) in Europe, Gams' "societies" (1932) which he included in a "federation" of *Ulotion;* (2) in France, Allorge's association (1921-22) of Ulota with *Orthotrichum lyellii*, as well as another association of *Orthotrichum obtusifolium* and *Tortula laevipila* with *T. papillosa*, *Radula complanata*, and *Leucodon sciuroides*, among others; and in Italy, Jaeggli's association (1933) of *Orthotrichum parvum*, with numerous other species of Orthotrichum, and *Leucodon sciuroides*, among other species. Since the Orthotrichum associations in Europe are generally characteristic of isolated trees along avenues, they seem more similar to the association of *Orthotrichum pumilum* of southern Michigan.

MIXED ASSOCIATIONS

That the interpretation of associations is somewhat arbitrary is indicated by the previous descriptions. The fact that many species appear in associations other than the ones they dominate and are even characteristic constitutents of these other associations, shows that the dividing line between associations is not sharp but that many of them intergrade. This is somewhat indicative of the various stages in the succession from one association to another. The occurrence of dominant species in other associations indicates that they can tolerate similar habitats. Consequently, this emphasizes the similarity of the tree bark habitats of a given region, the Upper Peninsula, for example. Many of these communities that have been designated as separate associations on the basis of representative samples may also be found in close proximity to other associations. For example, a mixed association of Neckera-Leucodon may be recognized in which Neckera and Leucodon are co-dominants. There are others in which Neckera and Porella, or Neckera and Anomodon are also co-dominants. These species are usually intermixed strand by strand, one growing above or below the other.

The key to the situation becomes evident in optimum habitats like those found at Miner's Falls, near Munising in the Upper Peninsula and in the Porcupine Mountains in the western Upper Peninsula.

The mist from Miner's Falls produces cool and humid conditions in a mature beech-maple woods. In addition to the beech and maple, the forest contains yellow birch, hop hornbeam, and hemlock with cedar restricted to the rock cliffs kept continually moist from the spray of the falls. A mature maple woods with the usual associated tree species (with the exception of beech which does not occur this far west in the Upper Peninsula) occurs in the Porcupine Mountains and at one place on the trail to Mirror Lake in a ravine with falling water, similar in coolness and humidity to the Miner's Falls habitat.

Quadrats taken on trees near breast height in these places showed all kinds of mixtures of the bryophytes, as well as definite representatives of the separate associations. Trees side by side and of the same species may have different associations. Thus, on one tree there might be a tangled mat of Neckera, Leucodon and Porella interwoven strand by strand.

As this mixture of the Neckera, Leucodon and Porella associations is the bark-inhabiting bryophyte community in Michigan of greatest coverage and vigor, it seems logical to designate it a mixed association.

Neckera and Leucodon are found so often together and the species in each association are so similar that it is certain that these mixed associations constitute recognizable communities in Michigan. This combi-

nation is not presented anywhere in the literature, although associations of Neckera and Anomodon, and Leucodon and Anomodon have been described separately.

Other Associations

Other associations of bryophytes on tree bark in Michigan are too fragmentary for detailed analysis, but do indicate possible community organizations. These include stands of *Drepanocladus uncinatus, Orthodicranum montanum, Dicranum viride, Hypnum reptile, Tortula papillosa,* and *Tortella tortuosa.*

Associated with Drepanocladus on northern white cedars in the Gorge near the University of Michigan Biological Station in the northern Lower Peninsula are *Lejeunea cavifolia, Neckera pennata,* and *Mnium ciliare,* whereas on the Islands the same tree species bears associations of *Lejeunea cavifolia, Lindbergia austinii, Neckera pennata, Dicranum viride* and *Pylaisia selwynii.*

Associated with *Orthodicranum montanum* on hemlock in the Upper Peninsula are *Pylaisia selwynii, Homomallium adnatum, Leucodon sciuroides, Frullania eboracensis* and *Ptilidium pulcherrimum.*

Associated with *Dicranum viride* on yellow birch in the northern Lower Peninsula are *Homomallium adnatum* and *Frullania eboracensis.*

Associated with *Hypnum reptile* on yellow birch and northern white cedar on the Islands are *Orthodicranum montanum, Orthotrichum sordidum, Frullania eboracensis, Ptilidium pulcherrimum* and *Ulota crispa.*

Associated with *Tortula papillosa* on American elm in the southern Lower Peninsula are *Lindbergia austinii* and *Orthotrichum pumilum.*

Associated with *Tortella tortuosa* also on American elm in the southern Lower Peninsula are *Orthotrichum pumilum, Lophocolea heterophylla* and *Encalypta streptocarpa.*

Succession Studies

Bryophytes that replace each other in a successional series on tree bark can be studied in at least two ways. One method would be to stake out permanent quadrats or squares on specific trees and to observe them over a period of years in order to see the changes as they occurred. Another and more convenient method is to compare young and old trees at the same time. However, the ideal is to select trees in which all possible factors are identical or similar except age so that any dissimilar results may be attributed to that single factor.

The comparative ages of trees in a given uniform habitat can be approximated by the diameter at breast height (DHB), if enough difference is allowed between those trees chosen as young and older to minimize local growth variations. This might be compared to succession studies of higher plants in which denudation occurred at intervals of several years, since the bark of a young tree presents a bare area for bryophyte colonization.

The comparison of trees from dissimilar habitats is not valid because of the different environmental factors which not only affect tree growth but also affect bryophyte development and distribution. But in a single locality where conditions are fairly uniform with respect to local climate, light, slope, soil and density of trees, such comparisons can be made more safely.

Studies of this sort were made in the upper peninsula of Michigan at three different places, Mt. Horace Greeley and Mt. Bohemia, Keweenaw County, and the Mirror Lake Trail in the Porcupine Mts., Ontonagon County (Fig. 1), all with climax forests of sugar maple. Chief trees associated with the sugar maple are hemlock, yellow birch, black ash, basswood, and northern white cedar.

To insure that the bryophytes were adequately sampled a preliminary study in each of the three regions using list quadrats of one square decimeter indicated that all the bryophyte species occurred in the first five quadrats, except for a few cases where up to seven quadrats were found necessary. Therefore in the more detailed coverage investigations ten quadrats on young trees and ten quadrats on older trees from each habitat were considered adequate.

On each tree the coverage of each bryophyte species was estimated to the nearest ten percent with the aid of a plastic frame cemented together, one decimeter square and divided into fifths by crosswires. The square decimeter of bryophytes was then collected and brought back to the laboratory for a closer study of the species under the dissecting microscope and for a closer check of coverage, which was considered an indication of dominance or control of the environment.

Greater uniformity of factors was obtained by selecting ten pairs of young and older trees practically side by side and over an area of ground essentially level and well within the forest. The difference in diameter between young and older trees was at least 9 inches to insure a decided difference in age. To minimize the difference between such factors of the micro-habitat as physical structure and acidity of the bark, exposure, moisture, and light, samples were taken from sugar maple trees only, on straight trees and always from the north side of the tree at breast height (4.5 feet from the ground). Trees with projections, knotholes or other unusual features at this spot were not selected. The important factors of time and chance were minimized by selecting only those trees which had chanced to have bryophytes on them and that had had time for these to develop into communities of some coverage. This was not too difficult since a majority of the trees in these moist habitats bore bryophyte communities.

The striking differences between bryophytes on young and older trees is apparent by a glance at Table 3.

TABLE 3. Species cover on young and older maples indicating succession.

	Location					
	Mt. Horace Greeley		Mt. Bohemia		Mirror Lake	
	Young	Older	Young	Older	Young	Older
AVER DBH INCHES	5	16	9	19	6	15
NUMBER OF TREES	10	10	10	10	10	10
Frullania eboracensis	1	X	1	..	3	..
Orthotrichum sordidum	2	..	3	..	3	..
O. elegans	..	..	3	..	..	..
Ulota crispa	..	..	1	..	1	..
Pylaisia selwynii	1	..	1	..	..	..
Neckera pennata	..	5	..	5	..	4
Leucodon sciuroides	..	5	..	5	..	1
Porella platyphylloidea	..	X	..	X	..	3
Anomodon minor	..	..	..	..	1	2

The figures in the body of the table represent coverage percentages according to the following scale:

X = present only
1 = 1- 20%
2 = 21- 40%
3 = 41- 60%
4 = 61- 80%
5 = 81-100%

These were obtained by averaging the percentage coverage of each bryophyte species on the ten young trees in each of the three habitats and on the ten older trees in each habitat and expressing this percentage as a figure according to the above scale. Since the Neckera, Leucodon and Porella were often intermixed strand by strand, it was impossible in some instances to estimate separate coverages so that the table indicates some coverages in excess of 100%.

Young maples have species of Orthotricha and Ulota with Frullania and Pylaisia, whereas older maples have Neckera, Leucodon, and Porella with some Frullania. In addition, the older maples have a higher coverage of species indicating a better community development. *Anomodon minor* is found on both young and old maples on the Mirror Lake Trail because of the somewhat better moisture conditions there, but is found more commonly on tree bases elsewhere in Michigan.

This investigation indicates that in these localities of Michigan, the hepatic, Frullania, is a pioneer on young maples but often persists in other communities, sometimes growing on the other bryophytes; Frullania is followed by the acrocarpous mosses, Orthotrichum and Ulota, and these in turn by Pylaisia; and the pleurocarpous mosses Neckera and Leucodon form a successful community on older maples with the hepatic, Porella, mostly growing on and over the other two.

Further investigations of the relationships of bryophytes in Michigan reveal they may be classified in two ways, according to successions and according to moisture requirements. Investigations and observations indicate that the pioneer association on young trees through the northern Lower Peninsula and northward is *Frullania eboracensis* (or some other species such as *Frullania asagrayana* or *F. bolanderi*). In some instances the Ptilidium association enters, most generally on conifers and particularly on balsam fir. The Radula association is also a pioneer, occurring simultaneously or at a slightly later stage than the Frullania.

The associations of Orthotrichum and Ulota generally need some sort of a projection, as a knothole for establishment, and develop generally pure stands that may exist for long periods of time, until some other associations become established through the usual succession stages and gradually invade the protuberances occupied by these associations. The species of *Orthotrichum* and *Ulota* may persist for a time as relics but are eventually crowded out by the Neckera, Leucodon or other associations.

The pioneer hepatic and acrocarpous moss associations are followed by the pleurocarpous moss associations. The moisture of the micro-habitat determines which of the pleurocarpous moss associations will come in next.

The pioneer hepatic and acrocarpous mosses occur in the driest habitats from Orthotrichum and Ulota to Radula, Frullania and Ptilidium. From xerophytic to less xerophytic, the pleurocarpous mosses are *Homomallium adnatum, Pylaisia selwynii, Leucodon sciuroides, Neckera pennata,* and *Anomodon minor.* The hepatic, *Porella platyphylloidea* is intermediate between Leucodon and Neckera in Michigan, often growing on and over the mosses.

Discussion and Conclusions

Communities of bark-inhabiting bryophytes are not always correlated with forest tree climaxes in Michigan because the tree climaxes are distributed over a wider variety of habitats than the bark communities. In habitats with optimum moisture conditions, certain bryophyte communities occur on all the tree species in that habitat. Under dry conditions, some bryophyte communities may show a preference for particular tree species.

Many bryophyte communities are much more widely distributed throughout the world than the tree species upon which they occur (as indicated in the association descriptions), since certain combinations of habitat conditions that can be tolerated by a given bryophytic community occur in forests of different types and on trees of different species.

Since the tree species is not the most important factor involved in the development and distribution of bark-inhabiting bryophytes in Michigan, the evidence for the influence of other factors is now presented.

On the basis of the distribution of bark-inhabiting bryophyte communities, Michigan may be divided into two parts. In the southern Lower Peninsula north to approximately latitude 43° North, the *Homomal-*

lium adnatum association and the *Orthotrichum sordidum* association are most common. North of this line, including the northern Lower Peninsula, Islands, and the Upper Peninsula, the mixed associations of Neckera-Leucodon-Porella are most common. This indicates that the bryophytes on tree bark may be more sensitive climatic indicators than the trees. Table 2 indicates the bryophyte associations on the different tree species in diverse habitats in various regions. The tree climaxes, for example, the beech-maple climax forest, occur in all regions; that is, in the southern Lower Peninsula, northern Lower Peninsula, Islands, and the Upper Peninsula. No bryophytes occur on beech in most of the habitats of southern Michigan, but bryophyte communties of good bark coverage, like Neckera, do occur on this species in the Upper Peninsula. Maple bears communities of *Homomallium adnatum* in the south and Leucodon and Neckera associations in the Upper Peninsula.

No instrumental measurements were made of the extremely small and diverse microclimates of the tree bark. However, much was learned of these microclimates by the indirect method of determining the relative requirements or tolerances of the various species of bryophytes for the habitats in which they grow. For instance, with respect to the moisture factor, *Anomodon minor* is generally found on the tree bases because they are moister, so that when this species occurs on the trunk proper, it indicates that the trunk in that place is moister than usual. This species is not correlated with tree species but with moisture, since it was found in all three regions on sugar maple and black ash; on beech only in the Upper Peninsula; on white oak in the southern Lower Peninsula; and in the northern Lower Peninsula and Upper Peninsula on hop hornbeam, northern white cedar and basswood. Other species, e.g., *Homomallium adnatum,* generally indicate drier conditions.

Different factors may be relatively more important at different stages of the life cycle of bark-inhabiting bryophytes as well as the life cycle of the whole bryophyte community. When the spores or gemmules are first shed they not only must become lodged on the bark to begin development, but also need more moisture.

The place of lodgement may be different for different bryophyte species. Species of *Ulota* and *Orthotrichum* in many instances seem to need projections to establish a foothold. The hepatics, *Frullania eboracensis, Radula complanata* and *Porella platyphylloidea,* and many of the mosses, as Homomallium can establish themselves on bare bark and often on the hardest-barked trees, probably during rainy periods. Certain other species may become lodged in the foliage of these bryophyte species. Soft-barked trees may afford a better place of lodgement but other factors are more important here as well, since in a moist habitat most bryophyte species can start on most tree species regardless of bark texture. Beech is generally considered to have a very hard and smooth bark and has no bryophytes in the drier places, as in the southern Lower Peninsula. In moist habitats as in the Upper Peninsula, however, beech is the host of well-developed Neckera associations, as well as others. On Mackinac Island and near Munising in the Upper Peninsula, beech has a well developed bryophyte flora centering around rough places in the bark caused by sun scald.

Once the spore or gemmule is lodged the moisture factor becomes relatively the most important in the development of the bryophyte species and communities. Therefore, any factor or factors that influence the amount of available water or evaporation of that water may become relatively more important from time to time.

Many of the bryophytes that ordinarily grow on the bark of living trees, occur also on rocks. *Neckera pennata* grows on bare rock completely devoid of humus in Wilderness Park, northern Lower Peninsula (and elsewhere). Other species, as Frullania, Porella, and Ptilidium occur frequently on Neckera, with no rhizoidal connection with the bark. Thus, in this region, the bark seems to be of importance chiefly as a means of support. Again, however, in the drier places, the bark may serve as a reservoir of water (particularly the softer barks), and thereby may increase the relative humidity of the microhabitat.

The collection of dust may influence the development of bryophytic communities, as along the roads on Mackinac Island, where much dust is raised by the horses and carriages. In places where other conditions are favorable, better development seems to result where dust is collected, chiefly by the species of bryophytes, however, and the species of tree is of no importance.

The local distribution of bark bryophytes indicates that wind is important chiefly through its limiting effect on moisture conditions. The prevailing winds in Michigan are from the west and the northwest. Where there is not enough moisture for development of bryophytes on all sides of the trees, as at Cross Village on Lake Michigan, western northern Lower Peninsula, *Frullania eboracensis* occurs only on the west and northwest sides of the trees, due to moist winds from the lake which drive rain against the trunks. In other places that are unsheltered, such as the bare limestone cliffs at Burnt Bluff on the west side of the southward extending Garden Peninsula, Upper Peninsula, probably the wind (which crosses no appreciable body of water here) and its effect on the evaporation rate prevents bryophytes from developing other than on the east side of the trees, away from the lake shore. Wind is of course also independent of tree species.

Near Ann Arbor, in the southern Lower Peninsula, is a mature beech-maple woods that is cool and dark, with standing water in many places most of the year. None of the beech or maple trees have bryophyte species on the trunk. Apparently the only difference between this woods and others which have well developed bark-inhabiting communities is a

lack of sheltering undergrowth. The undergrowth has been removed by grazing and allows air to circulate freely through the woods, increasing the rate of evaporation. Experiments by Ochsner (1935) and others have also indicated that air movement is very important. Even in a fine rain, the relative humidity may decrease to 60-80 per cent, if a light breeze is blowing. Alongside the Little Manistee River, northern Lower Peninsula, is a cedar stand, partly fenced against grazing cattle. All other factors are apparently identical. No bryophytes occur in the browsed portion that has no sheltering underbrush. In the ungrazed portion, luxuriant stands of Pylaisia and Frullania are found.

Bark-inhabiting bryophytes have considerable reaction upon the bark as they grow and develop, as observations under the dissecting microscope disclose. They absorb moisture and hold it better than the bare bark and thus increase the speed of the dissolving action of water. The bark under bryophyte communities is much more spongy, soft and flaky and enables new communities to establish themselves more easily. As the succession of bryophyte communities on trees progresses from one stage to another, each stage modifies the bark and microhabitat so that the next stage can become established. As Billings and Drew (1948) have pointed out, to a great extent this succession may be the result of natural ageing of the bark, also.

The microfauna that exist in and among bark-inhabiting bryophytes is quite extensive. The bryophytes afford a home for such fauna as small snails, spiders and various insect larvae. In turn the shells, decayed cocoons, and the like may be a source of some minerals to the bryophytes. Spiders which appeared in some of the capsules, particularly of *Orthotrichum,* by their movements could aid in spore dispersal.

Time and chance are undoubtedly extremely important even to the exclusion of all other factors. When we find practically identical trees side by side with all conditions of the habitat similar, one with and one without bryophytes, the only explanation seems to be that spores have not chanced to land in a favorable place on the barren tree at the right time. The bryophytes modify the microhabitat by shading the bark from the sun, thus lowering the temperature, as well as softening the bark so that more moisture may be retained. The lower temperature and additional moisture decrease the rate of evaporation so that the relative humidity of a microhabitat is higher where bryophytes occur.

Consequently, it can be concluded that tree species indirectly affect the bark-inhabiting bryophyte communities chiefly by their influence on available moisture (and pH, Billings & Drew, 1938) and that restriction to certain tree species is characteristic of the drier microhabitats. When the available moisture supply is optimum, any or all bryophyte associations may occur on all tree species. Thus an abundance of moisture can compensate for factors like low pH, smooth bark, youth of tree and openness of stand. This is empheasized by the occurrence of the bryophytes in this investigation (and in most other studies) on habitats like rocks.

SUMMARY

Twelve associations of bark-inhabiting bryophytes have been recognized in Michigan, the region of the study. Of these, the *Homomallium adnatum* association is the most wide-spread community in the southern Lower Peninsula whereas northward a mixed association of Neckera-Leucodon-Porella forms the stands of most extensive coverage and of most vigor.

Three regions were recognized for the investigation: (1) the southern Lower Peninsula, (2) the northern Lower Peninsula (including the Islands of Mackinac and Bois Blanc), (3) the Upper Peninsula, all approximately delineated by Thornthwaite (1948) on the basis of potential evapotranspiration and available moisture.

Pioneer species of bryophytes on the bare bark include: *Frullania* spp., *Radula complanata, Ptilidium pulcherrimum,* and *Homomallium adnatum.* In habitats of optimum moisture the pioneer species are replaced by *Pylaisia selwynii, Leucodon sciuroides, Porella platyphylloidea, Neckera pennata,* and *Anoymodon minor.* These species tolerate dry habitats in approximately the order in which they are listed; the pioneer species are naturally the most tolerant.

Associations of bark-inhabiting bryophytes are not always correlated with tree climaxes in Michigan since moisture is the most important factor in their development and distribution and similar moisture conditions may occur on trees of the same species in different regions, and on trees of different species in the same region.

Better conditions for bark-inhabiting bryophytes occur northward in Michigan. In proceeding northward, when a bryophyte species is first encountered it occurs on those trees with the softer bark Farther north the species may occur on all tree species, and at the northern limit of its range it occurs only on those trees with harder bark.

The bark is of importance to bryophytes chiefly as a means of support, since most species that occur on bark are also found on habitats other than bark, e.g. on other bryophytes or on rock.

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CHARACTERISTICS OF SOME GRASSLAND, MARSH, AND OTHER PLANT COMMUNITIES IN WESTERN ALASKA

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[1] The work on which this article is based was supported by the Arctic Institute of North America with funds provided by the Office of Naval Research. For numerous courtesies and facilities thanks are extended to the Arctic Institute of The Catholic University of North America and to various divisions of the U. S. Department of the Interior, including the Office of Indian Affairs, the Alaska Native Service, the Division of Territories and Island Possessions, the Mt. McKinley National Park staff, and the Alaska Railroad. The author is greatly indebted to Ernest Lepage, Ecole d'Agriculture, Rimouski, Quebec, for identification of species and for assistance in collecting data in the field; and to Capt. E. D. Churchill, U. S. Airforce, Washington, D. C., for assistance in collecting data in the field and in compilation work. For valued assistance in the identification of specimens thanks are due C. R. Ball, W. C. Steere, F. J. Hermann, J. R. Swallen, J. P. Anderson, G. A. Llano, H. T. O'Neill, and L. H. Jordahl.

INTRODUCTION

Comparatively little is known about the various kinds of plant communities in western Alaska, and still less about their characteristics such as the floristic composition, number of individuals, cover, frequency of constituent species, environmental relationships, geographic distribution, relationships to other communities, and plant succession (Hanson 1950a). Much more is known about the kinds of species and their distribution (Hulten 1937, 1940, 1941-1949, Anderson 1943-1950). Knowledge of the communities, including their characteristics, is important in many ways, such as in determining the interrelationships of the vegetation and the environmental factors and in the use and care of natural resources. The native vegetation can be used to indicate the suitability of the land for crop production, for location of homes, townsites, airfields, roads, railways, recreation areas, etc. The plant community is basic in the evaluation of vegetation for grazing by domestic livestock or by game animals, and in the study of many wildlife habitats (Aamodt & Savage 1949, Ellis 1949, Kellogg & Nygaard 1949, Elkins 1950, Murie 1950, Palmer 1945, Palmer & Rouse 1945).

Several months were spent during the summer of 1949 in various parts of Alaska in order to determine and distinguish between various kinds of grasslands and other communities, and to secure data on their characteristics. Special attention was directed to grasslands and sedge marshes.

In the present status of knowledge concerning the ecology of plant communities in Alaska it was deemed advisable to study, largely by quantitative methods, the vegtation in a number of scattered areas, rather than to conduct more intensive research in one or two places. Much intensive research in restricted areas is needed for more complete understanding of the communities. Raup (1941) stated that the floristic and community points of view have been separated too long, and that while much work has been done on the structure of arctic and subarctic communities in Europe it has hardly begun in America. Polunin (1950) indicated that floristic and taxonomic knowledge of Arctic plants is now sufficiently advanced so that phytogeographical studies can be carried on more advantageously. This statement can also be applied to the analyses of communities. The present investigation is more exploratory than intensively analytical. So little work has been done on Alaskan communities that it appears premature at this time to attempt a classification, or to establish definite successional sequences, or to indentify the communities in accordance with classifications of similar ones in Scandinavia and other European countries. A few similarities between communities in Alaska and those in other countries will be pointed out. Much can be learned from the utilization of these communities in other countries for application in Alaska. The most useful classification and descriptions in connection with this study were those by Nordhagen (1928, 1936, 1940, 1943) but others were also used such as DuRietz (1925b, 1930) Iverson (1936), Seidenfaden & Sørensen (1937), Sørensen (1941), Madsen (1936), Polunin (1934-1935, 1948), Rübel (1930, 1936), Shelford & Twomey (1941), Porsild (1937), and Braun-Blanquet (1932).

PROCEDURE AND METHODS

During the 1949 season most of the plants were identified in the field by Ernest Lepage. Both in 1949 and in 1950 herbarium specimens were secured of all plants of which the identification was doubtful and the aid of specialists was secured whenever necessary. Specimens have been deposited in the Langlois Herbarium of The Catholic University of America, the National Herbarium, the herbarium of J. P. Anderson at Iowa State College, and W. C. Steere's moss herbarium at Leland Stanford University

The characteristics of cover and frequency were determined by the point-contact method (Levy 1927, Hanson 1950a). The frame containing 10 rods was set 20 times in each stand, spaced about 15 feet apart on 1 or 2 lines located in the well-developed part of the stand, not too close to the edges. This gave a total of 200 points per stand. The greater the number of contacts, or "hits," of the rods with plants, the greater is the degree of cover. The relative area of bare ground is indicated in the tables by "no hits." Frequency is expressed in percentage, *e.g.*, if *Calamagrostis canadensis* was touched by one or more of the rods in 10 of the 20 sets in a stand the frequency would be 50 percent. The frame corresponds to the use of sample areas of rectangular shape.

In studying the soil profile the working depth (the depth to which a large number of roots penetrated) and the maximum depth (the greatest depth at which roots were found) of the root systems were usually determined. In many instances, however, these critical depths could not be determined because of water seepage or frozen ground. The color of the soil was determined according to the Munsell color standards (1936). Appreciation is expressed to Dr. C. E. Kellogg, Chief, and Kenneth Ableiter, U. S. Soil Survey, for suggestions in the study of soil profiles.

Major communities such as the several kinds of forest, shrub, grasslands, the tundra complex, strand zones, marsh and bog communities, or formations, associations, associes, etc., as used by Weaver & Clements (1938) are readily recognized in many areas. Minor and micro communities present greater difficulties in their recognition, delimitation, and characterization, as pointed out by Griggs (1934, 1936) and Raup (1941). The stand was taken as the unit of study, as done by Hanson & Whitman (1938), Nordhagen (1928, 1943), and many others, especially in Europe. Usually a stand is readily recognized because it consists of a homogeneous, or relatively homogeneous, grouping of species on an area. The stand usually has a characteristic, fairly uniform appearance, or physiognomy, such as a zone of beach ryegrass, an alder thicket on a mountain slope, etc. Vegetation ordinarily consists of a more or less in-

tricate mosaic of stands, and is not a chaotic mixture of species. Within a certain stand there is considerable uniformity in soil and moisture conditions, topography, insolation, and other environmental factors. A stand is usually formed by several to many species, with one or a few species dominant in each layer. The grouping of species into stands is due to differences in environmental conditions in various areas and to differences in the ecological amplitude, or tolerances in various species. The species with similar or overlapping amplitudes tend to be associated in sites where the environmental conditions lie within their requirements. Species with widely different tolerances do not usually grow together in sites that have restricted ranges of environmental conditions. In some areas, such as hummock or tussock marsh or heath or where frost action is pronounced, the physical conditions vary considerably within small distances, sometimes within only a few inches, so that the vegetation units may be very small. Such areas have been designated as *mosaics* by Nordhagen (1943) and others, and might be considered as mosaics of microstands. In this sense the term *mosaic* appears to be useful in designating certain kinds of vegetation in Alaska. Vestal (1938) used *mosaic* for plant communities "obviously compound, not only as to layers, but as to differences in character among plants within a layer—the different kinds of vegetation making up the individual patches being repeated over the general area, so that the common expressions 'essentially uniform,' 'more or less uniform,' can still be applied to the mosaic as a whole" (p. 107). The term *vegetation-components* as used by Vestal may be useful in referring to the various kinds of communities which make up the mosaic.

In naming the communities an attempt has been made to use the dominants of one or more layers, determining the dominants largely on the basis of a high degree of cover and frequency. These communities, based upon the analyses of concrete stands, are basic in understanding the vegetation because they are the units of the major communities.

The stands were numbered in the order in which they were studied in the field, and these numbers have been retained in this paper in order to avoid error. The stands were located in the northeastern part of Kodiak Island, in the vicinity of Homer on the Kenai Peninusla, at Eklutna and Goose Bay on opposite sides of Knik Arm at the head of Cook Inlet, in the lower and upper Matanuska Valley, in the Talkeetna Mountains north of Palmer, near the mouth of the Delta River, at Eagle Summit, Kotzebue, near Healy, and in the Mt. McKinley National Park. Supplementary studies were made in the summer of 1950 at Homer, Eklutna, the Matanuska Valley, Healy, Nome, and in Mt. McKinley National Park (see map).

ENVIRONMENTAL DATA

Northeastern Kodiak Island

The town of Kodiak is situated near the northeastern end of Kodiak Island, an island comprising 3588 square miles (Capps 1937). The Naval Air Base is about 5 miles west of the town. Kodiak is on the shore of the northeast part of Chiniak Bay, into which several smaller bays, including Womens, Middle, and Kalsin Bay open. Dense Sitka spruce forest is found northeast and east of Kodiak, but westward the forest soon becomes scattered into thickets of spruce, willows, alders, cottonwood, elderberry, and other shrubs, with grassland between. The estuaries are covered mostly with dense stands of sedges and grasses. At the higher elevations dwarf heath shrub is common.

A major soil factor is the presence of ash near the surface. Georgeson and White (1924, pp. 2-3) described the deposition as follows;

> "On June 6, 1912, the dormant volcano known as Mount Katmai, on the Alaska Peninsula, suddenly became active and threw out enormous volumes of ashes, which covered the country and sea for thousands of square miles. The northern end of Kodiak Island was covered with an ash deposit to an average depth of 18 inches, and the Kodiak station, although 100 miles from the volcano by airline, was totally submerged. Vegetation was buried, all pasture was destroyed for the time, and cattle were on the verge of starvation." By July 1914 "The ashes had washed from the hillsides and settled in the hollows, and much of it had been carried to sea. Layers varying from 6 inches to 2 feet on the level ground developed an intricate network of cracks and crevices through which the native vegetation asserted itself. As a result, the extensive area, covering several thousand acres, in the station reserve was enabled to furnish sufficient feed for the herd, and during the remainder of 1914 and in 1915 the animals were thrifty. . . ."

Griggs (1918) described in detail the rapid recovery of the vegetation on the ash.

At Kodiak the mean annual precipitation is about 60 inches. The driest months are March to July inclusive, but there are more than 3 inches of precipitation each month of the year. The mean annual temperature is about 41° F., the August mean 50° F., and the January mean 29.5° F.

The Cook Inlet Basin

Except for the Homer area, which lies close to the Gulf of Alaska, and therefore has more of a marine type of climate and reflects more directly the influence of the Japanese Current, the Cook Inlet Basin shows considerable uniformity in climatic conditions. The most pronounced characteristics are the dry period in spring and early summer, the rainy period during the summer and early autumn, the cold and drying north or northeast winds, the warm and moist south or southeast winds, and the great variability in the weather from day to day, and from year to year.

At Homer the mean annual precipitation is 27 inches, the driest period extending from March through July. The mean annual temperature is 38° F., the August mean 55°, January 30°. The length of the frostless period from 1939 to 1946 ranged from 93 to 116 days. The mean annual precipitation at Anchorage is about 14.5 inches, the driest period

February to June. The mean annual temperature is about 35° F., the August mean 55.5, January 13.5. The length of the frostless period from 1939 to 1946 ranged from 115 to 143 days (Climatological Data). In the Matanuska Valley the mean annual precipitation varied from 15.5 to 18 inches in different sections. The driest period was similar to that at Anchorage. The mean annual temperature was 34° F. to 36.5, the August mean about 55, and the January mean 13 to 14. The average length of the growing season varied from 73 to 150 days at one station.

Miscellaneous Stations

At Kotzebue, located on the spit at the northwestern end of Baldwin Peninsula (Fig. 1) the annual precipitation is about 9 inches, the driest period November through June. The mean annual temperature is about 23° F., the August mean 48.5, January about -8°F.

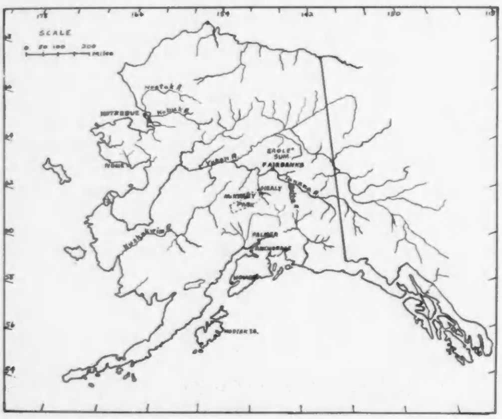

FIG. 1. Map of Alaska showing features for locating communities that were studied.

At McKinley Park, in the eastern end of Mt. McKinley National Park the average annual precipitation is about 14.5 inches, with December-May as the driest period. The mean annual temperature is about 28° F., the August mean about 46.5, January about 3.

The mean annual precipitation at Big Delta, near the junction of the Delta and Tanana rivers, is about 11 inches, the driest period extending from October through April. The mean annual temperature is about 30° F., August mean about 54, January -2.5.

SEQUENCE OF COMMUNITIES FROM ELYMUS MOLLIS TO MEADOW ON SANDY SEACOASTS AND ESTUARIES IN SOUTH CENTRAL ALASKA

This section includes the stands on gravelly and sandy sea beaches and estuaries in which *Elymus mollis* is the sole or one of the dominants, and the stands which show considerable resemblance to these, or which may have developed from them. The summarized results of the analyses of cover and frequency have been arranged in Table 1, in a sequence from the pioneer and least developed stands (19, 35) at the left, to the most developed, and presumably the oldest, at the right (40, 39). These stands were situated on Kodiak Island and on the shores of Cook Inlet and Knik Arm.

STAND 19 ELYMUS MOLLIS-LATHYRUS MARITIMUS

This stand was situated about six feet above the high tide line on an elongated ridge or dune composed of coarse argillite and graywacke sand and gravel, on the northwest side of Isthmus Bay, a part of Kalsin Bay southwest of Kodiak (Fig. 1). On the gently sloping sandy beach between the dune and the sea, above the reach of ordinary high tides, *Arenaria peploides* was abundant, *Mertensia maritima* and *Senecio pseudo-arnica* were scattered. Landward from the dune was a broad grassy, meadow-like area which sloped gradually to a marsh which drained into Kalsin Bay. This dune and the adjoining land evidently had connected a former island with the mainland, thus partly separating Isthmus Bay from Kalsin Bay. Beach dunes, similar to this one, with marshland or small lakes inland, were seen in a number of places on the shores of Chiniak Bay where headlands had been connected to each other, or islands connected with the mainland. This dune on Isthmus Bay was exposed to the full force of the storms from the south or southeast. The dune had an abrupt seaward slope, the top was covered with numerous, interlaced huge logs and other driftwood. The dune was covered with a dense growth of *Elymus mollis* and *Lathyrus maritimus,* and an occasional plant of *Arenaria peploides.* The first two had frequencies of 100% each, but Lathyrus with its broad leaflets, made up about 75% of the cover. Elymus stalks averaged about 3.5 feet tall on June 30, 1949. Lathyrus was mostly decumbent, some stems rising to about 14 inches, and was blooming.

The surface of the ridge was covered with a 1- to 3-inch layer of dead leaves and stems, under which was mostly rounded pebbles of argillite and graywacke, with scattered shells and quartz particles, up to 0.5 inch in diameter. This material was very loose to a depth of 42 inches, the depth to which the trench was dug. The gravel and sand particles fell down from the sides of the trench as soon as they became dry, leaving the roots and rhizomes hanging down. The gravel was almost dry at the surface, becoming moister with depth so that at 27 inches it was wet. Finely branched roots were numerous throughout, live rhizomes of both species were mostly in the upper 11 inches; dead Elymus rhizomes were numerous to 30 inches. The Elymus roots were white and about 1 mm. in diameter, except in the 3- to 6-inch terminal portions which were about twice as thick. These ends were very tender and covered densely with root hairs, to which gravel and sand particles adhered very closely, often forming depressions in the roots. Particles were appressed closely also to the terminal parts of Lathyrus roots.

TABLE 1. Sequence of Communities from *Elymus mollis* to Meadow Communities on Sandy Seacoasts and Estuaries

Species	Stand 19 Kodiak		Stand 35 Homer		Stand 7 Kodiak		Stand 14 Kodiak		Stand 5 Kodiak		Stand 4 Kodiak		Stand 23 Kodiak		Stand 40 Eklutna		Stand 39 Eklutna	
	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %
Elymus mollis	338	100	v.a.		365	100	137	90	122	85	3	5	19	45	88	80	1	5
Festuca rubra			s.		213	85	53	35	29	30	4	20	125	80	341	85	221	75
Festuca altaica									180	90	473	90						
Calamagrostis canadensis							208	90	235	90	347	95	92	55			1	5
Calamagrostis inexpansa															x			
Hordeum brachyantherum							97	45					84	95	16	25	64	80
Poa eminens			s.		43	45	3	10					2	5	3	5		
Poa palustris															5	5	184	85
Poa pratensis													120	70				
Poa hispidula			s.															
Deschampsia beringensis							2	5					3	5				
Trisetum spicatum							x											
Agrostis sp													58	70	16	30		
Hierochloe odorata															2	5	x	
Agropyron trachycaulum															403	100	x	
Phleum pratense																	x	
Carex cryptocarpa					60	50	4	5			3	5					x	
Carex gmelini			s.										9	15				
Carex glareosa																	1	5
Carex hindsii													x					
Carex sp.															22	45	5	15
Carex sp.																	x	
Luzula multiflora							19	25					1	5				
Lathyrus maritimus	883	100	s.										269	95				
Lathyrus palustris													x		127	95	349	100
Arenaria peploides	3	5											1	5				
Arenaria lateriflora									2	5			8	20				
Stellaria humifusa					111	85												
Stellaria longifolia													1	5	2	5	5	5
Stellaria laeta							x											
Plantago juncoides					25	20												
Cochlearia officinalis					2	10												
Lupinus nootkatensis							67	35					368	90				
Equisetum arvense							37	25									215	70
Achillea borealis							61	45	18	35	25	30	255	100	189	100	114	75
Solidago ?							8	15	25	50	31	55						
Polemonium acutiflorum							5	5			8	10						
Epilobium angustifolium							4	20			8	15						
Conioselinum benthami			s.				2	10					x		12	35	x	
Rhinanthus borealis							1	5					10	15	21	20	19	35
Cicuta sp.									3	10								
Galium boreale									4	5								
Trientalis europaea arctica							x		3	5	18	30						
Sanguisorba sitchensis											8	10						
Fritillaria camtchatcensis											1	5					x	
Viola langsdorfii											x							
Angelica lucida							x				x							
Potentilla pacifica							x								x		22	50
Ligusticum hulteni			s.				x						3	15				
Geum macrophyllum							x											
Ranunculus bongardii							x											
Cardamine umbellata							x											
Veronica serpyllifolia							x											
Prenanthes sp.							x											
Arabis hirsuta													2	5				
Gentiana sp.													x					
Castilleja unalaschkensis													x					
Taraxacum sp.													x		50	70	7	20
Dodecatheon macrocarpum															67	70	520	100
Hedysarum alpinum americanum															22	30	x	
Smilacina stellata															17	20	x	
Iris setosa															2	10	23	20
Aster junciformis															x			
Aster junceus																	x	
Triglochin maritima																	8	30
Habenaria dilatata chlorantha																	1	5
Parnassia palustris																	x	
Salix bebbiana																	x	

Species	Stand 19 Kodiak		Stand 35 Homer		Stand 7 Kodiak		Stand 14 Kodiak		Stand 5 Kodiak		Stand 4 Kodiak		Stand 23 Kodiak		Stand 40 Eklutna		Stand 39 Eklutna	
	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %
Polytrichum sp.	....	....	....	....	....	....	25	20	24	20	33	25						
Hypnaceae spp.	....	....	....	....	....	....	142	85	184	95	158	90	177	95	x			
Sphagnum sp.	....	....	....	....	....	....	....	....	....	....	2	5						
Hepaticae sp.	....	....	....	....	....	....	....	....	....	....	63	35						
No hits	....	....	....	....	5	....	2	..	1									
Total number of hits	1224	....	....	....	819	....	875	....	829	....	1185	....	1607	....	1405	....	1760	

FIG. 2. *Elymus mollis-Lathyrus maritimus* dune (Stand 19) connecting a former island, in the background, with the mainland. Plants on the beach are *Arenaria peploides* and *Senecio pseudo-arnica*. Isthmus Bay, Kodiak Island, June 30, 1949.

Some of the nodules on older roots were as much as 3 mm. in diameter. The numerous roots were very effective in binding together the sand and gravel. The dense cover afforded good protection against erosion by wind or water, and was effective in catching windborne material, thus increasing the height of the dune. The roots and rhizomes provided much protection to surfaces that had become exposed. The Elymus plants adjusted themselves to the increasing height of the dune by sending out new roots and rhizomes at higher levels. The decumbent stems of Lathyrus readily produced new roots when covered with a small amount of gravel or sand. The rhizomes are white and tender, and have a taste resembling young pea pods. The dead roots, rhizomes, and nodules add much organic matter to the sand and gravel.

No ash was seen in this dune from the beach sand to the seaward margin of the zone of large driftwood, a distance of about 40 feet, but at the landward side of the large driftweed (20 feet farther), ash was found below a 3-inch layer of gravel. At the top of the dune (12 feet farther inland), where the driftwood was scattered, the top 12 inches consisted of gravel, then an ash layer of 11 inches, with gravel below. *Calamagrostis canadensis* was abundant in this place, and the following were scattered: *Elymus mollis, Epilobium angustifolium, Heracleum lanatum, Lupinus nootkatensis,* and *Equisetum arvense.* About 22 feet farther inland (94 feet from the beach) the profile showed a 0.5-inch layer of dense, fibrous plant material, 2.5 inches of gravel, 14 inches of ash, with gravel below. The vegetation consisted chiefly of *Calamagrostis canadensis,* and scattered plants of the species listed above except *Elymus mollis,* and with the addition of *Castilleja unalaschkensis, Angelica lucida,* and young *Picea sitchensis.* Under a 60- to 65-year old Sitka spruce (age determined with increment borer), farther inland, and where the elevation was about 5 feet lower than the top of the dune, the uppermost 0-3 inches of soil consisted chiefly of spruce needles and partly decomposed organic material, then a horizon at 3-18 inches of light brown to light gray ash, at 18-18.75 inches partly decomposed needles and Equisetum stems, the remains of the vegetation covered by the ash fall in 1912, below which was gravel. The chief plants under the spruce in 1949 were Equisetum. This spruce tree, and evidently others nearby had started to grow about 25 years before the fall of the ash and had survived it. These profile descriptions indicate how much sand and gravel had been blown in from the beach since 1912, adding 3 inches to the soil at a distance of 60 feet from the beach, 12 inches at 72 feet, and 2.5 inches at 94 feet.

STAND 21 ELYMUS MOLLIS-LATHYRUS MARITIMUS

This stand was situated at the head of Kalsin Bay on a dune-ridge, 3 to 4 feet above the reach of ordinary high tides. This dune was much better protected from winds and storms than the one at Isthmus Bay where Stand 19 was located. The material in the dune consisted of finer particles, mostly less than 0.5 mm. in diameter. The vegetation was very similar to that in Stand 19, chiefly *Elymus mollis* and *Lathyrus maritimus.* Both were blooming on July 1, 1949; the spikes of Elymus were 42 inches high, the general height of the leaves about 25 inches, and Lathyrus extended up to about 14 inches.

STAND 35 ELYMUS MOLLIS

Near the southwestern end of the Kenai peninsula, near Homer, a spit about 4 miles long extends from the mainland southeastward into Kachemak Bay, which opens into the lower part of Cook Inlet. The western part of the spit is the highest part, with steep, eroding banks toward the bay. The eastern side, on which deposition is occurring, slopes gently from the dune-like western side to marshy land, especially at the landward end of the spit. The western side has the form of a broad ridge and was covered mostly with *Elymus mollis.* Other species, more numerous on the gently sloping eastern part, were *Lathyrus maritimus, Ligusticum hulteni, Carex gmelini, Festuca rubra, Poa eminens, P. hispidula,* and *Conioselinum benthami.* Some of the species found on the west shore below the dune, subject to overflow by higher tides, were *Arenaria peploides, Senecio pseudoarnica,* and a few plants of *Elymus mollis, Achillea borealis,* and *Lupinus nootkatensis.* Strong westerly winds blow sand and gravel from the beach and from the eroding west side of the dune to the top and eastward of the dune, much of the material being intercepted by the tall and dense stand of Elymus, which on July 7, 1949, was 4 to 5 feet tall. The highest parts of the dune were 8 to 10 feet above high tide line.

The most significant features of the soil profile were 1) the alternation of loose sand and gravel with organic, mucky material, indicating former surfaces for longer or shorter periods at depths of 8, 17.5, and 21 inches, 2) a deposit at 18.5-21 inches resembling volcanic ash, 3) the large number and deep penetration of roots, working depth at 48 inches, maximum below 55 inches, 4) the deep burial of rhizomes at 24 inches, 5) the soil profile data supports the evidence indicated by topography, by the erosion on the western side and deposition on the eastern side, and by land survey records (Jorgensen 1949), that the spit has and is continuing to move northeastward.

STAND 7 ELYMUS MOLLIS-FESTUCA RUBRA

This stand was situated near the lower end of the estuary at the head of Anton Larsen Bay on Kodiak Island. It was studied on June 23, 1949. Stands of this community alternated with stands of *Carex cryptocarpa* community on slightly lower areas. This community was reached usually by storm tides, but the Carex community was covered more frequently. As shown in Table 1, only 7 species were hit in this stand, the chief one being *Elymus mollis,* which made up nearly half of the cover. *Festuca rubra* made up about one-fourth of the cover. The stalks of Elymus were 24 to 30 inches high, the other grasses only 3 to 4 inches high, with occasional leaf blades to 12 inches, and flower stalks up to 18 inches. Although the stand appeared very dense (Fig. 3) much of the ground was bare, the total number of hits being only 820, as compared to 1225 in Stand 19.

The most important features of the soil profile were 1) the apparently rapid incorporation of residual herbage, which formed a layer up to 6 inches thick, and silty material into soil, 2) the adjustment of underground plant parts to the deposition on the surface, 3) the ash deposit, 10.5 inches thick below a 2-inch organic layer, 4) the fibrous and mucky horizon at 10.5-22 inches, formed prior to the 1912 Katmai eruption, very likely under a stand of *Carex cryptocarpa,* 5) gravel and sand below 23 inches, 6) working depth of roots at 26 inches, roots scarce below 33 inches.

FIG. 3. Soil profile and vegetation in the *Elymus mollis-Festuca rubra* community (Stand 7). Above the 10.5-inch layer of ash is a 2-inch horizon of organic material, mucky peat-like material below the ash. Anton Larsen Bay estuary, Kodiak Island, June 23, 1949.

The presence of Elymus in the mounds and ridges of the estuary was related to the sandy nature of the ash near the surface and the resulting better drainage. The mounds and ridges probably formed from sand blown up from the nearby beaches, and the process appeared to be continuing as shown by the ash grains in the surface 0-2 inches.

STAND 14 ELYMUS MOLLIS-CALAMAGROSTIS CANADENSIS

This community occurred on low broad ridges and mounds, 1 to 3 feet higher than the rest of the marsh on the estuary at the head of Middle Bay on Kodiak Island. The stand, studied on June 26, 1949, had more species than the preceding stands in this sequence (see Table 1). The stand could be recognized readily from a distance by the bluish green color. For several weeks in June the lupine flowers gave the vegetation a purplish blue color. Blow-out spots

were scattered in areas grazed by livestock. The abundance of Elymus appeared to be associated with the depth of the accumulation of ash. This ash evidently had been washed down from higher elevations and piled by the winds into low dunes. Additional important species were *Hordeum brachyantherum, Lupinus nootkatensis,* and various mosses. There were 16 species of flowering plants, the total number of hits was 872. As shown in Table 1 there were 12 additional species in the stand that were not hit.

Outstanding features of the soil profiles were 1) the fairly tough sod, due to the numerous, thick rhizomes and the very numerous roots of *Elymus,* 2) beneath a thin layer of moss was a half-inch organic layer and underlying layers of loose ash to a depth of 28 inches, 3) plant remains buried by the ash at 28-28.5 inches, 4) mucky material with some silt and scattered argillite pebbles below the ash to 44 inches, probably formed under a *Carex cryptocarpa* community, 5) working and maximum depths at 28.5 inches.

STAND 5 CALAMAGROSTIS CANADENSIS-FESTUCA ALTAICA-ELYMUS MOLLIS

This stand (Fig. 5) was typical of the community about half a mile from the shore on the estuary of Anton Larsen Bay, Kodiak Island. It was on slightly higher land where the ash was thicker than in the following stand which was adjacent. It was studied on June 22, 1949. The 3 species named above made up about 65% of the cover. As shown in Table 1, there were only 10 species of vascular plants, and only 829 hits, compared to 1185 in the following stand.

Important features of the soil profile were, 1) beneath a 1.5-inch layer of litter was a well developed 0-1.25-inch horizon, consisting mostly of organic material with scattered ash grains, 2) primary and secondary ash layers, 24.75 inches thick, 3) indications of a temporary surface horizon at 13.5 inches, 4) remains of vegetation growing prior to 1912 at 25 inches, 5) water level at 32 inches, 6) the large number of roots to 32 inches, 7) the peat-like deposit at 25-32 inches, formed probably under a *Carex cryptocarpa* marsh before the ash fall. The Carex community developed on a rocky and gravelly substratum, now at a depth of 32 inches.

STAND 4 FESTUCA ALTAICA-CALAMAGROSTIS CANADENSIS

This community (Fig. 6) was typical of the lower areas between the low mounds and ridges occupied by the preceding type, about one-fourth mile inland on the estuary of Anton Larsen Bay, on Kodiak Island. It was studied on June 22, 1949. *F. altaica* and *C. canadensis* provided nearly 70% of the cover. Mosses also covered much of the ground. The cover was greater than in the preceding community, 1185 compared to 829 points. There were 14 species of vascular plants, 12 of which were hit.

Characteristic features of the soil profile were 1) the development since 1912 has been rapid, as indicated by the 0-1.5-inch horizon beneath a thin compact layer of plant debris and moss, 2) a much thinner ash deposit, 9.5 inches, than in the preceding stand, 3) the 1912 surface at 11 inches, 4) the mucky silt layer at 11-21.5 inches, formed probably under a *Carex cryptocarpa* community, 5) water level at 17 inches, 6) roots numerous to 17 inches, 7) gravel below 21 inches.

FIG. 4. Result of trampling by cattle on a low *Elymus mollis* dune, exposing the loose ash to erosion. Middle Bay estuary, Kodiak Island, June 25, 1949.

STAND 23 LUPINUS NOOKATENSIS-LATHYRUS MARITIMUS-ACHILLEA BOREALIS-POA PRATENSIS-FESTUCA RUBRA

This well developed stand (Fig. 7) was situated on the estuary at the head of Kalsin Bay, Kodiak Island, on a low, broad ridge about 300 feet inland from the beach dune described under Stand 21. The slope was gradual toward the shore. The 5 species listed above on July 1, 1949, accounted for about 70% of the cover. Mosses also occupied much of the ground. Other important species were *Calamagrostis canadensis, Hordeum brachyantherum,* and *Agrostis* sp. Elymus was scattered. The presence of *Poa pratensis* was probably due to seeds introduced when a livestock experiment station was located in this vicinity. The total number of vascular species was 25, 19 of which were hit, large compared to previous stands in this sequence. The ground was well covered by vegetation as shown by the large number of hits, 1607. The occurrence of 8 grass species, 2 sedges, and Luzula was noteworthy. The high frequencies of many species indicated considerable uniformity in the stand. The high state of development was apparently due to the favorable soil condition.

Significant features of the soil profile were 1) the tough sod, suitable for the construction of a roadway, 2) ash limited to small pockets in the 0-1.5-inch organic layer, the rest washed or blown away probably a short time after falling, 3) alternating layers of sand and gravel between 1.5 and 42 inches, 4) roots very numerous, especially in the finer material, working depth at 28 inches, maximum 40 inches, roots have great influence on soil-binding and soil-development (Fig. 7).

FIG. 5. *Calamagrostis canadensis-Festuca altaica-Elymus mollis* community (Stand 5). The organic surface horizon 1.25 inches thick, ash horizon to depth of about 25 inches, below which is peaty material formed in marsh (probably *Carex cryptocarpa*) prior to 1912. Anton Larsen Bay estuary, Kodiak Island, June 22, 1949.

STAND 22A CALAMAGROSTIS CANADENSIS

This community, examined on July 1, 1949, occurred on slightly higher land on the Kalsin Bay estuary than the preceding. The most abundant and dominant species was *Calamagrostis canadensis.* The more common associated species were *Hierochloa odorata, Elymus mollis, Equisetum arvense, Carex* sp., *Lupinus nootkatensis, Lathyrus maritimus,* and *Angelica lucida.* The soil profile consisted of a 0-3-inch organic horizon with much sand and gravel, ash between 3 and 5 inches, sand at 5-17 inches, and gravel below.

FIG. 6. Stand 4, *Festuca altaica-Calamagrostis canadensis* community on lower areas than Stand 5 (Fig. 5), organic surface layer 1.5 inches thick, ash layer 9.5 inches, mucky peaty material below 11 inches formed prior to 1912. June 21, 1949. Anton Larsen Bay estuary, Kodiak Island.

STAND 22B CALAMAGROSTIS CANADENSIS

This stand was located on the edge of an eroding bank on the Kalsin Bay estuary, about 2 or 3 feet higher than the preceding stand. *C. canadensis* was the dominant. Other prominent species were *Elymus mollis, Epilobium* sp., *Achillea borealis, Poa* sp., *Festuca rubra, Lathyrus maritimus,* and *Carex gmelini.* It was examined on July 1, 1949. The inch-thick surface organic layer was underlaid by ash to 14 inches, below which was an alternation of sand and gravel layers. Roots were numerous to 26.5 inches, working depth at 41 inches, maximum 65 inches.

FIG. 7. Stand 23, *Lupinus nootkatensis-Lathyrus maritimus-Achillea borealis-Poa pratensis-Festuca rubra* community on a low ridge on the Kalsin Bay estuary, Kodiak Island. Ash is limited to a few pockets in uppermost half inch. The roots are very effective in binding the sand and gravel which occurs in alternating layers to depth of 42 inches. July 1, 1949.

STAND 40 AGROPYRON TRACHYCAULON-FESTUCA RUBRA-ACHILLEA BOREALIS-LATHYRUS PALUSTRIS

This and the following stand were situated on the almost level, extensive meadows lying between Knik Arm and the Chugach Mountains, east of Eklutna, about 20 miles northeast of Anchorage. These meadows produce forage of excellent quality, and hay has been cut on parts of them. The surface of the meadows varied only slightly in elevation. Broad

areas, a foot or two higher than the shallow depressions, were cut across by occasional natural or artificial channels, some of which were several feet deep. Water is backed up by the highest tides into the channels, and then floods some of the lowest areas, leaving behind a deposit of light gray silt after receding. The lowest parts remain wet much later in the spring than the higher areas. A number of plant communities were recognizable on the ground and on aerial photographs. Two examples of these on higher ground were studied on July 11, 1949, and again in July-August, 1950, when the entire area of the meadows was studied fairly intensively and the communities mapped. Stand 40 is representative of about the final stage in the sequence from the Elymus dune community to meadow. Stand 39 is included in this sequence because of its resemblance and proximity to Stand 40, but it probably belongs more properly in the sequence of *Carex cryptocarpa* marsh to meadow. It is important in showing convergence of the two series to meadow. Stand 40 is typical of drier areas, Stand 39 of moister areas.

The surface of Stand 40 was almost level and had not been covered by floods in recent years. The 4 species named in the title of this stand made up about 76% of the cover. Other important species were *Elymus mollis, Dodecatheon macrocarpum,* and *Taraxacum* sp. In places *Poa palustris* and *Hordeum brachyantherum* had much greater cover and frequency than in this stand. Additional research is needed to determine the interrelationships of these species and the relations to the substratum. A total of 22 species was noted, 19 of which were hit. The growth of moss was very sparse (Table 1).

Important features of the soil profile were 1) the uniformity in color and texture, the horizons being recognizable more by "feel" than by appearance, 2) lamination below 24 inches, due to deposition of silt following periods of flooding, 3) considerable modification by roots, rhizomes, nodules, etc., of the upper horizons to a depth of 24 inches, 4) nodules to 10 inches, 5) deep penetration and large number of rhizomes and roots, working depth of roots at 36 inches, maximum 60 inches, 6) neutral soil reaction, 7) most suitable of any of the lowland soils for tillage, provided drainage is adequate. Because of the importance of this community the soil profile is described in detail below.

The surface was covered with a loose layer, 3 to 4 inches thick, of dead leaves and stems, mostly grass, with moss scattered in the lower part, lowermost portion partly decayed.

0-1 inch. Very dark gray, silt loam, the rather loose, granular aggregates held in place by the very numerous live roots and rhizomes, nodules numerous, moist, pH 6.8-7.0.

1-24 inches. Dark gray with some gray horizontal and diagonal streaks, silt, a few fine gritty particles, picks out in irregular blocks and plates which crumble readily, upper 8 inches less compact than the lower part, roots and rhizomes very numerous in the upper 9 inches, numerous below, nodules to 10 inches, apparently much organic matter in the upper 9 inches, moist, pH 7.2.

24-60 inches. Dark gray, silt with fine gritty grains, much more compact than horizons above, shows lamination due to deposition following floods, mottled with brown, occasional lenses of fine sand, picks out in thin to thick platy structures which break down to thinner plates; very similar to the 10-48-inch horizon in Stand 39; number of roots decreases gradually below 10 inches, working depth at 36 inches, many roots to 48 inches, a few live roots at 60 inches, pH 6.8-7.0.

STAND 39 FESTUCA RUBRA-POA PALUSTRIS-FORBS

This stand was representative of the vegetation occurring in broad depressions, slightly lower than the preceding community, on the extensive meadows east of Eklutna. It appears that this community does not become flooded now by high tides backing water into the drainage channels, but the water does remain later in the spring than on the higher ground. In June and July large tracts of this community are brilliant with the red flowers of *Dodecatheon macrocarpum.* Other forbs, including *Lathyrus palustris, Equisetum arvense,* and *Achillea borealis* contribute much to the cover, but later in the summer, the grasses *Festuca rubra, Poa palustris,* and, in places, *Hordeum brachyantherum* become conspicuous. In some areas *Poa palustris* is the sole dominant. The vegetation is dense and the cover is complete as indicated by the unusually high cover index of 1760 hits (on July 11, 1949). The total number of species

FIG. 8. Stand 39. *Festuca rubra-Poa palustris*-Forbs in the meadow land east of Eklutna. *Dodecatheon macrocarpum, Achillea borealis,* and *Iris setosa* are conspicuous. Roots numerous to 25 inches, a few to 48 inches, in soil developed from silt deposited from flood waters of Knik Arm. July 11, 1949.

noted in this stand was 30, 18 of which were hit (see Table 1). This stand afforded common ground for the association of species from communities of higher and lower elevations, and from earlier and later stages in succession, such as *Carex cryptocarpa*, *C. glareosa*, and *Triglochin maritima* from lower areas; and *Agropyron trachycaulum*, *Hordeum brachyantherum*, and *Elymus mollis* from higher areas.

The soil profile resembled that in the preceding stand. The chief difference was that only the upper 10 inches of this one were about as well developed as the upper 24 inches in Stand 40, and the working depth of the roots was shallower, 25 inches, compared to 36 inches.

DISCUSSION OF THE SEQUENCE FROM ELYMUS MOLLIS TO MEADOW COMMUNITIES

The course of succession on sandy and gravelly shores begins just above ordinary high tides with the invasion of species which are tolerant to a high degree of salinity, such as *Arenaria peploides*, *Mertensia maritima*, *Senecio pseudo-arnica*, and *Elymus mollis*. The first invaders are usually scattered, forming only fragments of communities, but they aid in causing the deposition of wind-borne sand and gravel so that a dune is formed in time. As the dune becomes higher *Elymus mollis* becomes denser and other species appear, especially *Lathyrus maritimus*, in places *Poa eminens*. They are accompanied by species from earlier and later stages, forming the *E. mollis* and *E. mollis-L. maritimus* communities. As shown in the descriptions of the soil profiles organic matter gradually accumulates in the soil due to the death and decay of numerous roots, to plant debris on the surface, and to the deposition of plant parts by floods. This kind of invasion, development of communities, and formation of beach dunes is characteristic of, and widespread, on Alaskan shores, such as the Gulf of Alaska, Norton Sound, Kotzebue Sound, etc. Similar communities occur on the shores of Baffin Island, northern Quebec, Southampton Island (Polunin 1948), Greenland (Trapnell 1933), northwestern Europe (Warming 1909a, 1909b, Iverson 1936, Nordhagen 1939-1940, Westhoff 1947), etc.

Elymus communities can be recognized readily from the air because of their distinctive bluish green color. Communities, or community fragments, of single species or mixtures of *Arenaria peploides*, *Mertensia maritima*, and *Lathyrus maritima* are widely distributed in the Arctic from northwestern Alaska to Iceland, Spitzbergen, northern Scandinavia, the White Sea, etc. (Uphof 1941, Tolmatchew 1934).

In south-central Alaska early and common invaders in the Elymus communities are *Festuca rubra*, *F. altaica*, *Calamagrostis canadensis*, *Hordeum brachyantherum*, *Achillea borealis*, *Lupinus nootkatensis*, *Polytrichum* spp., and other mosses, so that mixed grass-forb communities develop. Good examples of these, which might be grouped into a larger Elymus-Festuca-Calamagrostis-Forb class are Stand 7 (*Elymus mollis-Festuca rubra*), Stand 14 (*E. mollis-Calamagrostis canadensis*), and Stand 5 (*C. canadensis-F. altaica-E. mollis*). The number of species may become large in comparison with the earlier stages as in Stand 14 with 27 vascular species. In these intermediate stages the soil material has become stabilized, the influence of the sea has diminished, and the soil profile may show considerable development, as in Stand 23. The grazing value of this type for cattle and horses is high, especially for winter pasturage.

The final herbaceous stage in this sequence is probably similar to Stand 40 (*Agropyron trachycaulum-Festuca rubra-Achillea borealis-Lathyrus palustris*), which has a well developed profile as shown by the blocky and platy structure, and organic content to a depth of 24 inches. Abundance of *Poa palustris*, as in Stand 39, apparently indicates somewhat moister sites, and such stands probably fit better into the next sequence. Willows are usually among the first woody invaders into these lowland meadows. Polunin (1948) described stands on the northern slopes of Quebec and elsewhere in the Canadian Arctic, located inland from Elymus stands, as containing more species than those nearer the sea, and evidently were more meadow-like. In places the transition from the Elymus communities was directly to Dryas barrens, or to salt marsh in sheltered muddy situations. This has also been observed on the shores of Seward Peninsula. Iverson (1936) in Denmark, Cederkreutz (1927) in South Finland, Nordhagen (1939-1940) in Norway, and others, have analyzed meadows which resemble stands 39 and 40 near Eklutna. Westhoff (1947) described successional sequences similar to this on several Dutch islands.

SEQUENCE OF COMMUNITIES ON SILTY ESTUARIES AND COASTS

This section includes analyses of stands and descriptions of zonations on silty estuaries and coasts, in which *Puccinellia phryganodes* is one of the most important pioneers in invading the muddy substratum which is inundated frequently by tides. The course of succession from the pioneer communities is to sedge marsh, grassland, and finally to woody vegetation. The pioneer stages and sedge-marsh communities are very different from the early stages in the preceding sequences, but there is increasing convergence in the later stages; as illustrated by stands 23, 22A, 40, 13, 32. Analyses of stands in this sequence are given in Table 2. The stands and zones were located in south-central Alaska, on Kodiak Island, and on the shores of Cook Inlet and Knik Arm. Zonations at Goose Bay on Knik Arm and near Homer will be described first because of the number of successional stages that occur in them.

ZONATION ON THE GOOSE BAY ESTUARY

The Goose Bay estuary occupies a large area on the north side of Knik Arm, north and slightly east of Anchorage. The eastern part of the estuary, with steep banks that extend a few feet above the usual

TABLE 2. Sequence of Communities on Silty Estuaries and Coasts.

Species	Stand 15 Kodiak		Stand 57 Goose Bay		Stand 58 Goose Bay		Stand 59 Goose Bay		Stand 41 Knik Flats		Stand 6 Kodiak		Stand 11 Kodiak		Stand 12 Kodiak		Stand 13 Kodiak	
	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Stalks	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %
Carex cryptocarpa	138	90	2	5	4	5	270	100	1830	100	2965	100	553	100	43	50	174	75
Carex ramenskii			78	80	1935	100	74	20										
Carex pluriflora					4	10	808	100										
Carex glareosa							71	45							1	5		
Carex canescens													57	30			26	25
Carex macloviana																	x	
Eriophorum scheuchzeri													10	10			x	
Luzula multiflora																	x	
Juncus filiformis													7	10				
Juncus balticus															467	100	23	10
Puccinellia glabra	18	40									91	40						
Puccinellia triflora									x									
Poa eminens	3	10	389	100	5	15	11	35	11	10					11	30	1	5
Poa sp.																	5	10
Festuca rubra	2	10													130	40	44	45
Elymus mollis	4	10													2	5		
Calamagrostis deschampsioides					x		3	15										
Calamagrostis canadensis													213	85	62	85	540	100
Hierochloe odorata									x									
Deschampsia beringensis													18	30	253	90	57	35
Hordeum brachyantherum															37	25	30	30
Phleum alpinum																	19	5
Poaceae sp.									2	10								
Plantago juncoides	218	90	58	55														
Stellaria humifusa	122	70	3	15	12	40	6	30			52	20						
Triglochin maritima	20	15	579	100	172	90	82	75	39	50					1	5		
Triglochin palustris	8	20	49	50	11	5			x									
Potentilla pacifica	76	75	204	100	141	95	188	100	5	10					63	70		
Chrysanthemum arcticum			3	5			4	5										
Lathyrus maritimus					x													
Lathyrus palustris							12	10	x						97	75		
Galium trifidum							6	10	1	5			4	10	8	25	8	10
Trientalis europaea arctica							4	5							1	5		
Cicuta mackenzieana							x		x									
Cicuta douglasii																	1	5
Ranunculus cymbalaria									2	5								
Cochlearia officinalis											64	50						
Epilobium seedlings													7	20				
Epilobium angustifolium																	5	10
Equisetum sp.													3	5	23	25		
Equisetum arvense boreale																	145	75
Lupinus nootkatensis															10	10		
Ligusticum hulteni															7	10		
Achillea borealis																	3	10
Geum macrophyllum																	3	10
Solidago ?																	7	10
Sanguisorba sitchensis																	3	5
Rhinanthus borealis																	4	5
Athyrium filix-femina																	x	
Hypnaceae spp.													180	90	194	100	200	100
Salix sitchensis																	x	
Salix fuscescens							35	25							4	5		
Alnus fruticosa																	x	
No hits	5		2										1					
Total number of hits	609		1365		2284		1574		1890		3172 stks.		1052		1414		1298	

high tides, is eroding, due to the undermining effect of waves and tides, and of currents from the outflow of the Matanuska and Knik rivers. Deposition is occurring in the western part of the estuary and a stream winds through approximately the central part. The estuary extends a considerable distance inland, gradually becoming narrower. Many of the streams flowing into Knik Arm are heavily loaded with fine glacial material, so great quantities of silt are deposited on the shores, as well as on the bottom.

Zonation is well developed on the estuary. The zones vary considerably in width, depending chiefly

upon the gradient in elevation, with resulting differences in frequency and depth of flooding, salinity, drainage, rate and depth of deposition, etc. On areas where the gradient is small, many minor zones can be recognized. Where the gradient is steeper the minor zones merge into major zones. The following major zones were recognized and detailed analyses were made in several of them.

ZONE 1 PUCCINELLIA PHRYGANODES-SALICORNEA HERBACEA-SUAEDA MARITIMA

This outermost zone is subject to frequent tidal submersion. It has a fine silt substratum which is very slippery to walk on but it is firm enough so that one does not sink in. Characteristic species were *Puccinellia phryganodes,* the most common first invader, *Salicornea herbacea, Suaeda maritima,* and in the upper portion scattered tufts of *Puccinellia triflora.* Additional species were *Glaux maritima, Spergularia canadensis,* and a few which were more typical of higher zones such as *Triglochin maritima, Plantago juncoides,* and *Elymus mollis. Carex ramenskii,* growing from tufts washed down from higher zones, was found occasionally. Mats of dark green algae grew in places. *Puccinellia phryganodes* usually formed mats which greatly facilitated walking. This plant is particularly well suited to this substratum because the runners grow rapidly and take root readily. The plants are also able to tolerate tidal and wave action.

ZONE 2 PLANTAGO JUNCIOIDES-PUCCINELLIA TRIFLORA-P. GLABRA

This zone was about 2 feet above ordinary high tides. Surface drainage was fairly good and the compact fine silt was easy to walk on. The most characteristic and abundant species was *Plantago juncoides.* The chief associates on the lower ground were *P. triflora* and *P. glabra;* on the upper part *Triglochin maritima.* Other species were *Elymus mollis* on many scattered mounds; *Salicornea herbacea* which formed reddish spots especially in poorly drained areas, surrounded by the dark bluish green of Puccinellia; and *Triglochin palustris, Ranunculus cymbalaria, Potentilla pacifica, Atriplex gmelini, Poa eminens,* and *Chrysanthemum arcticum.* This zone was very wide in places and much of the ground was bare.

An example of this community, Stand 15, on the outer part of the estuary of Middle Bay, Kodiak Island, was studied on June 27, 1949. The first invaders were usually scattered on the part of the shore which was frequently covered by high tides. Stand 15 was located on slightly higher land where aggregation had started. Only 10 species were recorded. The cover was rather sparse, 609 hits. The chief species were *Plantago juncoides, Stellaria humifusa, Carex cryptocarpa,* and *Potentilla pacifica;* which made up 92% of the cover. The presence of *Carex cryptocarpa* and *Elymus mollis* was due the chunks of sod, rhizomes, etc., which had been washed in. These chunks had become centers of aggregation favoring the development of later stages. Many of the species in this community made adjustments to the deposition of silt, pebbles, etc., by the formation of new roots and rhizomes at successively higher levels and by the upward growth of old rhizomes. Stellaria adjusted itself to new levels by the creeping stems, Plantago stems elongated and produced new roots at higher levels, Potentilla produced many runners, and Carex readily formed roots at higher levels. These plants were very important in the stabilization of the surface soil. Trafficability was good where the plants covered much of the ground.

Important features of the soil profile were 1) the recent deposition of silt, argillite pebbles, jelly fish, etc., on the moderately firm surface, 2) the adjustment of the roots and rhizomes to the deposition, 3) the thick deposit of ash at 2-24 inches, 4) water level at 16 inches, 5) working depth of roots at only 9.5 inches, some large live roots at 16 inches, 6) old plant crowns at 7.5 inches.

ZONE 3 TRIGLOCHIN MARITIMA-POTENTILLA PACIFICA

This zone, compared to the preceding, was on slightly higher land. It had a firm compact, fine silt substratum, fairly well drained. The characteristic species were *T. maritima* and *P. pacifica.* Other prominent species were *T. palustris, Carex glareosa,*

FIG. 9. Stand 57. *Triglochin maritima-Poa eminens-Potentilla pacifica* in Zone 3 on the Goose Bay estuary. Leaves of *Potentilla* and a head of *Chrysanthemum arcticum* are conspicuous. Soil consists of 22 inches of firm silt upon saturated peat, roots numerous to 22 inches. July 16, 1949.

Poa eminens, and on wetter spots *C. ramenskii.* The zone was 2 to 3 rods wide along the eroding bank in the eastern part of the Goose Bay estuary.

Stand 57 was located in this zone. On July 16, 1949, *T. maritima* had spikes up to 3 feet tall, *Poa eminens* inflorescences were 2 to 3 feet tall, *Chrysanthemum arcticum* and *Potentilla* were blooming. Although only 9 species were recorded the cover was good, 1365 hits. The surface was firm, much firmer than zones farther inland, due to the good drainage.

Outstanding features of the soil profile were 1) the deposit of 22 inches of silt with intermixed plant debris upon saturated peat. The face of the eroding bank, 16 feet away, showed alternations of coarse driftwood and silt for 10 feet below the peat, 2) the peat layer at 22-27 inches was probably formed when the shore had eroded less than at present and consequently was more poorly drained, 3) the rapid dimunition in number of roots at the top of the peat layer, working depth at 22 inches, maximum depth at 23 inches, 4) strong sulfur odor from the peat.

ZONE 4 ELYMUS MOLLIS

This zone with its tall growth of *E. mollis* was found on low ridges on the estuary and on higher banks along the stream. It belongs more properly in the first sequence, but is included here because it did occur on this estuary. The substratum was much drier, sandy, and better drained than that in the preceding zones. Important associates were *Festuca rubra, Parnassia palustris,* and *Dodecatheon macropum.* Many other species occurred, including *Hedysarum alpinum americanum, Achillea borealis, Lomatogonium rotatum, Conioselinum benthami, Lathyrus palustris, Ligusticum hulteni, Trientalis europea arctica, Carex gmelini, Hierochloa odorata,* and *Iris setosa.*

ZONE 5 CAREX RAMENSKII-TRIGLOCHIN MARITIMA-POTENTILLA PACIFICA

The next zone inland from Zone 3 varied in width, the ground was wetter than Zone 3 because of the poorer drainage, and it was probably less brackish. It could be readily recognized by its yellow green color. Stand 58, located in this zone had a dense cover, 2284 hits, *Carex ramenskii* making up about 84%. Only 8 species were recorded and 2 more were seen (Table 2) on July 16, 1949 (Fig. 10).

Outstanding features of the soil profile were 1) the large fiber content to a depth of 20.5 inches, 2) the very tough sod, about 3.5 inches thick, difficult to cut, heavy and firm, capable of sustaining a limited amount of traffic, 3) peat, with fragments of wood, between 20.5 and 28.5 inches, 4) water seepage reached level of 10 inches, 5) working depth of roots at 20.5 inches, maximum 21.5 inches, root growth evidently impeded by toxic substances in the peat, similar to that in Stand 57 in Zone 3.

ZONE 6 CAREX PLURIFLORA-C. CRYPTOCARPA

This zone was found in places on the estuary, especially adjoining Zone 5 in the eastern part, where Stand 59 was also located. On the landward side it

FIG. 10. Stand 58. *Carex ramenskii* community in Zone 5 on the Goose Bay estuary, showing *Potentilla pacifica* scattered among sedge stalks. Numerous roots and rhizomes in the silt soil to depth of 20.5 inches, water level at 15 inches. July 16, 1949.

adjoined the *Myrica gale-Calamagrostis* zone. It was wetter than the preceding zone. On July 17, 1949, the color was bluish green, in contrast to the yellowish green *Carex ramenskii* and the purplish Myrica-Calamagrostis zones. The leaves of *C. cryptocarpa,* extending to 3 feet, were taller and more wavy than those of *C. pluriflora.* The fruits were ripening on all the sedge species at this time. *C. pluriflora* formed about half the cover with a total of 1574 hits in Stand 59. *C. cryptocarpa* grew mostly in the wetter spots and was much less numerous. As shown in Table 2, there were 15 vascular species, 14 hit. Other prominent species were *Potentilla pacifica, Triglochin maritima, Carex ramenskii,* and *C. glareosa.*

Outstanding features of the soil profile were 1) beneath the 1-3-inch layer of dead leaves and stems was a tough fibrous silt layer, 15.5 inches thick, 2) peat layer at 15.5-25.5 inches, 3) water level at only 5 inches, 4) peat unfavorable for growth of roots, working depth at only 15.5 inches, maximum 19.5 inches.

ZONE 7 CAREX CRYPTOCARPA

This species formed almost pure stands in places that were wetter and more poorly drained than Zone 6. It formed extensive communities in many places on the shores of Knik Arm, as in the vicinity of Eklutna and on the Knik Hay Flats. In the eastern part of the estuary this zone varied considerably in width and alternated in places with zones 6 and 8.

Stand 41, located on the Knik Hay Flats is representative of the *Carex cryptocarpa* community which occurs in many estuaries, including the large marshy areas at the mouth of Eagle River on the south shore of Knik Arm, marshes in the vicinity of Homer, beaches in the vicinity of Anchorage, and many others. *Carex cryptocarpa* was replaced to some extent in spots where the water was more than 4 inches deep by *Triglochin palustris*. In shallow, fresh water ponds *Scirpus validus* formed dark green stands. On slightly higher land meadow communities, similar to Stands 39 and 40 were found. Willows and a few cottonwoods formed a fringing forest along streams. Portions of this Flat have been mowed or grazed in the past, mostly in connection with the development of the livestock industry in the Matanuska Valley. These uses have been restricted to a considerable extent, however, by various hazards, such as the presence of holes in which cattle bogged down, by floods covering parts and marooning the animals, by poor drainage, and by the abundance of mosquitoes at certain times. This stand studied on July 12, 1949, was subject to flooding at times. *C. cryptocarpa* formed an almost pure community, receiving 1830 of the total of 1890 hits. Only 6 other species were hit, and 5 additional were seen (Table 2, Fig. 11).

FIG. 11. *Carex cryptocarpa* community (Stand 41) showing alternation of silt and peat in the profile, much water seepage below 16 inches, roots numerous to 30 inches. Knik Flats on north side of Knik Arm, July 12, 1949.

Important features of the soil profile were 1) the alternation of silt and peat layers to the depth of 16 inches, caused probably by periods of flooding and poor drainage followed by periods of better drainage, 2) very tough sod, capable of supporting moderate amount of traffic, sod covered with 2-inch layer of loose leaves and stems, 3) water-saturated silt between 16 and 30 inches, 4) large number of live and dead roots to 30 inches, especially in the uppermost 10 inches (cf. Kellogg and Nygaard 1949, p. 49).

Stand 6, another example of this community, studied on June 23, 1949, was situated on the lower end of the estuary at the head of Anton Larsen Bay, Kodiak Island. Ordinary high tides entered only the lower parts, but storm tides covered all of it. Plants from this stand were invading the nearby beach by means of rhizomes, etc. On slightly higher areas *Elymus mollis* (see Stand 7) was dominant. *Carex cryptocarpa* occupied this stand almost to the exclusion of other species. The stalks were so dense and tall, 2.5 to 3 feet, that counting of stalks was more feasible than using the point-contact method. Twenty sample areas, each 1 x 3 feet, were located 15 feet apart on a line extending through the central part of the stand. The total number of stalks on the 60 square fet was 3172, consisting of 2965 stalks of *Carex cryptocarpa*, 64 of *Cochlearia officinalis*, 52 of *Stellaria humifusa*, and 91 of *Puccinellia glabra*. This method gave higher percentages of frequency for the less abundant species than the point-contact method (Table 2). Cochlearia and Stellaria were 1 to 3 inches tall, Puccinellia occurred only as seedlings.

Important features of the soil profile were 1) the scattered barnacle shells, Fucus plants, pieces of wood, etc., on the surface, and the nature of the 0-1-inch horizon indicated that deposition of water-borne and probably also wind-borne materials is occurring, 2) firm surface due to silt and the very dense growth of roots and rhizomes, 3) the thick ash deposit at 1-21 inches, upon gravel and sand, the primary layer probably deposited in a foot or more of bay water in 1912, 4) water level formed at depth of 20 inches, 5) roots penetrated to below 21 inches.

The detailed description of the soil profile shows the condition of the soil in large areas and the development since 1912.

The surface was covered with a thin felt-like mat of dead Carex leaves, scattered Fucus plants, mosses, green algae, some brown mucky material, barnacle shells, and argillite pebbles.

0-1 inch. Light gray, gray brown, and dark gray brown, sandy ash with small quantities of silt and organic matter in spots, apparently of recent deposition, few roots.

1-4 inches. Ash, gray to dark brown to reddish yellow, sandy with some intermixed silt and organic matter, wet, roots and rhizomes very numerous, most of *Carex* crowns in this horizon.

4-9.25 inches. Ash, gray to light gray with very many strong brown to reddish yellow mottlings, sandy with a little organic material, very numerous coarse roots about 2 to 3 mm. in diameter colored reddish yellow.

9.25-15 inches. Ash, very pale brown with brownish and reddish mottling, sandy, wet, roots numerous.

15-21 inches. Ash, light gray except for pink band at 18-18.25 inches, water seeped rapidly as soon as this horizon was dug into, silty material washed into pit very rapidly, dried into fine powder, compact in mass, roots numerous but fewer than in horizon above, pH 6.8.

Below 21 inches. Gravel and sand, argillite and slate with mostly rounded edges, water level at 20 inches, few roots.

Stands 26A and 26B examined on July 1, 1940, were representative of communities found

on low, poorly drained areas, near streams or channels, subject to flooding by high tides, on the estuary of Kalsin Bay, Kodiak Island. These poorly drained areas were mostly inland from the Elymus dune near the tide line. In 26A the most common species in addition to the dominant *Carex cryptocarpa* were *C. mackenziei, C. glareosa, Calamagrostis deschampsioides, Eleocharis kamtschatica, Potentilla pacifica, Triglochin palustris,* and *T. maritima.* The surface was covered with a thin mat of decaying leaves. The sod was very tough. The 0-3-inch horizon was brown, fibrous in upper part, mucky below. The 3-30-inch horizon was gray ash. It was too wet to dig below 30 inches.

Stand 26B, as compared to 26A, had greater abundance of *C. canadensis,* Potentilla, and *Lathyrus palustris,* but *Carex cryptocarpa* was the main dominant, Eleocharis and Triglochin were less abundant. The site was about 2 feet higher than the preceding stand, the water level a little deeper, and the surface was firmer. The sod was very tough. The 0-2.5-inch horizon was very fibrous; between 2.5-7 inches there was light gray to gray, sandy ash; at 7-10 inches brown mucky material; at 10-11 inches argillite gravel; and at 11-15 inches mucky material.

ZONE 8 CALAMAGROSTIS CANADENSIS-MYRICA GALE

This low shrubby community, was best developed in the wet, poorly drained land receiving seepage from the bank rising above the eastern part of the estuary. The most characteristic plant, *Myrica gale,* formed tussocks or hummocky areas, due to the stems growing first horizontally and then gradually ascending. Between the hummocks were depressions with water 2 to 12 inches deep. The Myrica stems were about 3 feet high. *Calamagrostis canadensis,* 4 to 6 feet high, was very abundant. The purplish color in the third week of July, 1949, was due to the inflorescences of *C. canadensis.* Low plants of *Salix fuscescens* were also abundant. The irregularity of the branching of Myrica and the scattered driftwood made walking very difficult. Ideal conditions for the breeding of mosquitoes were afforded by the water of different depths, and the variety of temperatures and light intensities. Additional species noted in this zone were *Lathyrus palustris, Trientalis europea arctica, Poa eminens, Carex pluriflora, Festuca rubra, Rumex fenestratus, Potentilla pacifica, P. palustris, Angelica lucida, Galium trifidum,* and *Hierochloa odorata.* This community resmbles Ostwald's (1923) *Myrica gale* association in the Komosse in Sweden.

Just below and on the lower part of the steep slope, adjoining the *Myrica gale* zone was a zone 2.5 to 4.5 feet high, consisting of *Epilobium angustifolium, Angelica lucida, Equisetum arvense, Calamagrostis canadensis, Rosa acicularis, Lathyrus palustris, Conioselinum benthami, Achillea borealis, Poa* probably *palustris, Rubus strigosus,* and *Trientalis europea arctica.* The woodland on the steep, west-facing slope consisted chiefly of *Betula resinifera, Alnus fruticosa, Populus tremuloides, P. tricocarpa* (?), *Salix bebbiana, Viburnum edule,* and many species from the zone below and from the forest above, including *Linnaea borealis, Geranium erianthum,* and *Pyrola asarifolia.* In small ponds on the estuary, usually in the *Carex cryptocarpa* zone, *Hippuris vulgaris* was abundant, surrounded by a zone of *Scirpus pacificus.*

Several communities were not seen in the zonation on the Goose Bay estuary but were studied elsewhere, and will be described here.

FIG. 12. Dairy cattle grazing chiefly *Carex cryptocarpa* on the estuary of Women's Bay, Kodiak Island, June 25, 1949.

STAND 11 THE CAREX CRYPTOCARPA-CALAMAGROSTIS CANADENSIS COMMUNITY

A large part of the estuary at the head of Middle Bay, as well as other estuaries on Kodiak Island, not occupied by trees and shrubs, was covered with this community. Much of the land was subject to flooding by high tides and storm waters. The lower parts were covered with a few inches of water. Stream channels and depressions were scattered over the estuary, so high water spread rapidly. The stand selected for analysis on June 25, 1949, was about half a mile from the high tide line. The surface relief varied slightly so that some of the sets of the point-contact frame were in water 1 to 2 inches deep. As shown in Table 2, *C. cryptocarpa* was the dominant species, receiving 553 of the total of 1052 hits. *C. canadensis,* occupying about half as much cover, was finding suitable places for invasion and, in time, as the soil became drier would replace the *Carex.* Mosses covered much of the surface. Only 9 vascular species occurred in this stand, among them *Carex canescens* and *Eriophorum scheuzeri.*

Important features of the soil profile were 1) the firmness of the surface caused by the dense mass of roots and rhizomes and the compactness of the soil, covered with about 2 inches of plant debris and dense moss, 2) recently deposited silt at 0-2 inches, 3) thick ash deposit at 2-19.5 inches, 4) water level at 13.25 inches, 5) working depth of roots at 12 inches, maximum 23 inches, 6) peat and mucky material at 19.5-32 inches, as deep as dug (cf. Kellogg & Nygard 1949, p. 66).

STAND 12 JUNCUS BALTICUS

The *Calamagrostis canadensis-Deschampsia beringensis-Juncus balticus-Festuca rubra* communities are represented by analyses of 2 stands, No. 12 in which *Juncus balticus* was the dominant, and No. 13 in which *Calamagrostis canadensis* was the chief dominant.

Stands in which *J. balticus* was the chief dominant were few and occupied only small areas on the estuary of Middle Bay, Kodiak Island. They were on slightly higher land than the preceding stand, and consequently the water level was deeper. The chief species were *J. balticus*, heading at 15 inches, *Deschampsia beringensis, Festuca rubra*, and mosses. The first three constituted about 60% of the cover. Other important species were *Lathyrus palustris, Potentilla pacifica, Calamagrostis canadensis*, and *Carex cryptocarpa*. As shown in Table 2, there were 18 vascular species, the cover index of 1414 hits was fairly high, almost 50% more than in the preceding stand.

Important features of the soil profile were 1) the sod, below the 2-inch layer of moss and plant debris, not so tough as where *Carex cryptocarpa* is dominant, 2) recent deposition of silt and plant debris in the upper 2.5 inches, 3) the thick ash deposit at 2.5-25 inches, in primary and secondary layers, 4) mucky material with slate and argillite fragments below 25 inches, 5) water level at 20 inches, 6) roots and rhizomes very numerous in the upper 2.5 inches, working depth at 12 inches, maximum at about 18 inches.

STAND 13 CALAMAGROSTIS CANADENSIS

Areas on the estuary of Middle Bay, Kodiak Island, occupied by *C. canadensis* as the chief or only dominant, were somewhat higher than those areas dominated by *Carex cryptocarpa* or *Juncus balticus*, and could be readily recognized by the yellowish green color as compared to the darker green of the other two. Sites intermediate in elevation contained larger proportions of the 2 latter species. This stand, representative of the higher and better drained parts of the estuary, not occupied by trees or shrubs, studied on June 26, 1949, was dominated by *Calamagrostis canadensis*, 1 to 2 feet high (Fig. 13). *Alnus fruticosa*, 4 to 5 feet high, partly dead, were scattered. Other important species were *Equisetum arvense, Carex cryptocarpa*, and mosses. The total number of vascular plants was 25, 19 of which were hit. The cover was moderately good, as indicated by the total of 1298 hits (Table 2).

Noteworthy features of the soil profile were 1) the tough sod, beneath the 1.5-inch layer of moss and plant debris, 2) the unusually well developed silt-loam horizon, rich in organic matter, at 0-5.75 inches, indicating rapid soil development during the past 37 years, 3) moderately thick ash layer at 5.75-15 inches, 4) remains of vegetation, buried by ash in 1912, formed a thin layer at 15 inches, 5) mucky material at 15.25-19.25 inches, formed probably in a saline marsh with shallow water, underlaid by strata of silt and gravel, 6) working depth of roots at 22 inches, maximum 29 inches.

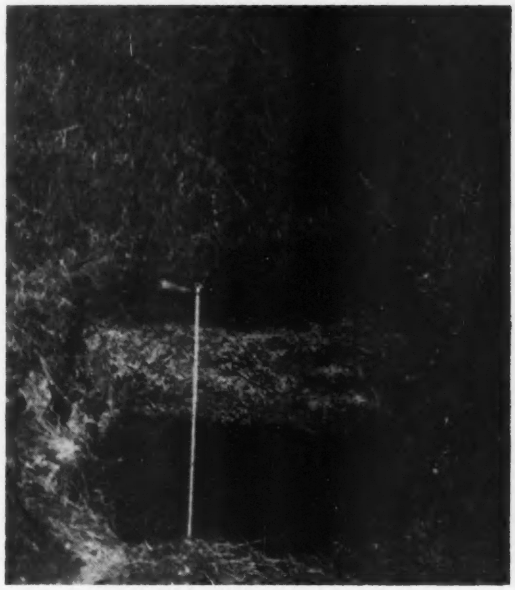

FIG. 13. *Calamagrostis canadensis* community (Stand 13) on estuary of Middle Bay, Kodiak Island. Small alder beyond the trench. Excellent soil development to depth of 5.75 inches since the ash layer at 5.75-15 inches was deposited in 1912, mucky organic material below the ash. June 26, 1949.

Meadow communities appear in the sequence on most estuaries but none were studied at Goose Bay. Examples of these communities are Stand 32, described below, and Stands 39 and 40.

STAND 32 FESTUCA ALTAICA

This stand, studied on June 19, 1940, was located on a nearly flat area in the upper part of the estuary at the head of Pasagshak Bay, Kodiak Island, about 350 feet from a stream which drained into a fairly large lake. The surface was slightly hummocky. The vegetation consisted of scattered bunches of *Festuca altaica*, and a thick layer of moss, chiefly *Pleurozium schreberi* and *Polytrichum* sp. Other species were *Calamagrostis canadensis, Epilobium angustifolium, Angelica lucida, Solidago* sp., *Sanguisorba sitchensis*, and a few invading shrubs of *Rosa acicularis* and *Sambucus pubens*. This stand resembled Stand 4 in the first sequence because of the presence of *Elymus mollis*. Both belong very likely more properly in this silty estuary sequence, as one of the final grassland stages before the shrubs invade.

The most significant features of the soil profile were 1) the shallowness of the gravel, at 14.75 inches, 2) the mucky surface layer was only 0.5 inch thick, 3) ash layers between 0.5 and 10.75 inches, 4) mucky material at 10.5-12.75 inches, with fine sandy clay below that to the gravel, 5) working depth of roots at 14.75 inches.

Marsh and meadow communities were being in-

vaded in many places by shrubs and trees such as willows, alders, and cottonwood. Examples of two woody communities are described below.

STAND 25 ALNUS FRUTICOSA

Alder thickets, varying in density and in the extent of area occupied, were scattered along streams in the Kalsin Bay estuary. This stand, studied on July 1, 1949, was near the *Calamagrostis canadensis* stand (22A) but slightly lower in elevation. The alders were 10 to 12 feet high. Sufficient light penetrated the canopy to permit the growth of fairly numerous shade plants, 3 to 4 feet high, of *C. canadensis.* Less numerous were *Epilobium angustifolium,* 3 to 3.5 feet high, *Luzula multiflora, Equisetum arvense, Achillea borealis, Stellaria sitchana,* and *Carex brunnescens.* Important features of the soil profile were 1) the thin ash layer between 0.75 and 6.75 inches, covered by a silty ash organic horizon, consisting mostly of roots, 2) plant debris and moss formed a layer 1 to 2 inches thick on the surface, 3) below the organic layer at 6.75-7.25 inches, the 1912 surface layer, was a horizon of gravel, 4) roots most numerous at 0-1, and 7.5-11 inches.

STAND 8 POPULUS TRICOCARPA

This type of forest is usually preceded in succession on estuaries by alder and willow thickets. An extensive forest with *Populus tricocarpa* as the major dominant, covers a large part of the inner end of the estuary at Anton Larsen Bay, Kodiak Island. This forest, studied on July 3, 1949, was usually open, but varied greatly in density. In places the trees were so widely scattered that grassland was more prevalent than forest. The tall cottonwoods were usually 1 to 2 feet in diameter, but a few were as much as 4 to 6 feet. A second layer of woody plants, 5 to 10 feet high, was present in many places and consisted of *Sambucus racemosa pubens, Rosa acicularis, Viburnum edule, Populus tricocarpa,* and *Picea sitchensis.* The herbaceous layer, 3 to 5 feet high, was made up chiefly of *Calamagrostis canadensis* and *Epilobium angustifolium,* but included a number of other species such as *Cicuta douglasii, Athyrium filix-femina, Heracleum lanatum, Deschampsia beringensis, Veratrum eschscholtzia, Delphinium glaucum, Carex macrochaeta,* and some shrubs, usually rose. In the low herbaceous layer at 6 to 12 inches the most numerous were *Trientalis europea arctica,* and *Dryopteris disjuncta.* Less numerous were *Arenaria lateriflora, Polemonium acutiflorum,* and *Pyrola asarifolia incarnata.* The fern, *Dryopteris austriaca,* was seen growing in the crotch of a large cottonwood.

Important features of the soil profile were 1) the surface organic layer only 1 inch thick below the 2-8-inch litter layer, 2) the thick ash deposit at 1-23.5 inches, consisting of primary and secondary layers, 3) remains of vegetation buried by the ash in 1912 at 23.5-24.5 inches with silt below this to the gravel at 28 inches, 4) indications of leaching at 1-1.5 and at 24.5-26 inches, 5) the deep penetration of large roots, the deep working depth at 29 inches, and a few roots at 36 inches, 6) the survival of the cottonwoods following the thick deposition of ash.

ZONATION ON THE BEACH OF KNIK ARM EAST OF ANCHORAGE

The first invaders on the fairly firm, very gently sloping silt beach east of Anchorage along Knik Arm, as observed in August, 1950, were *Puccinellia phryganodes, P. triflora,* and *Triglochin maritima.* The outermost plants, scattered on the beach and subject to frequent overflow by high tides, formed a zone up to about 10 feet wide. Often this zone was not present, and a zone, dominated by *Triglochin maritima,* 1 to 2.5 feet high and dark bluish green in color, formed a sharp ecotone with the bare silt of the strand (Fig. 14). Interspersed with the seaside arrow-grass were *T. palustris, Puccinellia phryganodes, P. triflora,* and in the inner part of the zone were *Carex cryptocarpa* and a few plants of *Scirpus pacificus.* The substratum in these two zones was compact silt, slippery when wet. The mats of *Puccinellia phryganodes* offered much resistance to erosion and were often surrounded by silt deposits. The outer border of the *Triglochin maritima* zone often ended in a sharp escarpment 6 to 12 inches above the bare strand, caused apparently by waves. Small pieces of driftwood were scattered among the plants.

FIG. 14. *Triglochin maritima* zone on the firm silt shore of Knik Arm near Anchorage. Aug. 7, 1949.

The *Carex cryptocarpa* zone consisted chiefly of a dense growth of *Carex cryptocarpa,* 12 to 18 inches high. In the outer part *Triglochin maritima* and *T. palustris* were scattered; in the inner part *Calamagrostis canadensis, Chrysanthemum arcticum,* and *Potentialla pacifica.* Driftwood was scattered. The silt was firm and usually well drained on the surface.

Farther inland was a zone characterized by the lighter green, dense growth of *Calamagrostis canadensis,* 1 to 2 feet high, with many yellow flowered plants of *Potentilla pacifica.* Less numerous were *Poa eminens* 2 feet tall, *Triglochin palustris, Carex cryptocarpa, Rumex* sp., *Scirpus pacificus,* and *Oxycoccus microcarpus.* The silt soil was firm and there was much driftwood, including many large logs washed ashore by storm waves.

Adjacent to this zone was one dominated by *Calamagrostis canadensis,* about 6 feet high, and *Myrica*

gale, about 5 feet high. The surface was hummocky and the depressions wet and boggy. It was difficult to walk through. In the outer parts of this zone *Angelica lucida* and poison hemlock, *Cicuta douglasii,* up to 6 feet high, were scattered. Occasional alders, up to 8 feet high, Alaska birch, about 3 feet high and *Equisetum* sp. were seen. The presence of alder and birch may have been due to filling in of soil near the inner part of this zone for a roadway. Before the construction of the road the Calamagrostis-Myrica community had covered apparently most of the wide lowland between the water and the steep bluff covered with forest. Part of the lowland, near the bluff was also occupied by trees, including Alaska birch, spruce, alder, and willows.

Zonation Along Shore of a Small Bay Near Homer

This bay, just south of Homer, is almost entirely surrounded by land, only a narrow strait at its southwestern end connecting it with Kachemak Bay and Cook Inlet. During low tide most of the silt bottom is exposed and water is found in only small basins and drainage channels. Studies were made here in July, 1949, and in August, 1950. Zonation was well developed on the very gently sloping northern part of this area (see Fig. 15), but the areas occupied were not as large as at Goose Bay.

FIG. 15. Zonation on shore of a small bay at Homer, beginning in the foreground 1) *Puccinellia phryganodes* and *Triglochin maritima,* 2) *Carex ramenskii* and *Triglochin palustris,* 3) *Carex cryptocarpa,* 4) *Calamagrostis canadensis,* 5) *Salix* spp., 6) *Picea sitchensis.* The bluffs are covered chiefly with *Calamagrostis canadensis, Epilobium angustifolium, Alnus* sp., and *Picea sitchensis.* July 7, 1949.

At the lowest level, on the wet, fairly firm silt, the most abundant plant was *Puccinellia phryganodes,* the first species to invade the mud. The rapid growth of these widely branched, creeping stems formed rather open mats which made walking easy. *Triglochin maritima* and *Plantago juncoides* were scattered. This zone was subject to overflow by some of the tides.

The most abundant and dominant species in the next higher zone the *Carex ramenskii-Triglochin maritima* zone, yellowish green in color, was *Carex ramenskii,* with scattered patches of *C. mackenziei* and tufts of *Triglochin maritima.* The substratum was wet, but firm, so walking was easy. In places the dominant was *Triglochin maritima,* 1 to 2 feet high, with interspersed plants of *Plantago juncoides* and *Puccinellia phryganodes. Triglochin* plants gave this community a dark green color.

The next higher zone, dominated by *Carex cryptocarpa,* 1 to 2.5 feet high, was darker green than where *Carex ramenskii* was the chief dominant. The substratum was wet. Occasional pools of water and logs were scattered. A few plants of *Calamagrostis deschampsioides* and *Potentilla palustris* were also scattered. The soil profile consisted of a surface horizon, 10 inches thick, of fibrous material mostly, dark brown, saturated with water. Below this the color changed gradually to very dark gray at 18 inches, where the material was clay. Water seeped rapidly into the trench 6 inches below the surface. Live roots were very numerous to 16 inches, and scattered in the clay at 18 inches.

The next zone was rather narrow, consisting of dense growth of mostly *Calamagrostis canadensis.* On July 7, 1949, it was 4 to 5 feet high and yellowish green in color. On August 5, 1950, it was 5 to 6 feet high and purplish green due to the inflorescences. Earlier in the year the yellowish straw of preceding years growth gave the characteristic color. The tall grass of the current year, the straw, the hidden logs and stumps, wet spots, etc., make trafficability very poor. More or less scattered were *Polemonium acutiflorum, Equisetum fluviatile, E. arvense, Trientalis europea arctica,* and *Rumex* sp.

The next zone consisted mostly of willows, *Salix barclayi* and *S. pulchra,* 10 to 15 feet high. *Calamagrostis canadensis* and *Equisetum arvense* were abundant among the willows. The thicket-like growth was dense and difficult to walk through.

Bordering the willow zone was the forest of *Picea sitchensis,* with intermixed *Betula resinifera* (?), ranging up to 60 feet high. In places *Calamagrostis canadensis* and *Epilobium angustifolium* made dense stands, 5 to 8 feet tall, which effectively concealed logs and stumps.

Discussion of the Sequence from Puccinellia Phryganodes to Meadow, and Cottonwood Forest Communities on Silty Estuaries and Coasts

Invasion of the silty substratum of estuaries begins on areas that are inundated daily by tides. The following species occurred as scattered individuals or community fragments; *Puccinellia phryganodes* forming mats by its extensive runners and apparently growing rapidly, *Salicornea herbacea,* and *Suaeda maritima.* A little higher on the beach, but still subject to inundation were *Puccinellia triflora, Glaux maritima, Spergularia canadensis, Arenaria peploides,* and occasionally accidentals from higher zones, such as *Triglochin maritima, Plantago juncoides, Cochlearia officinalis, Carex cryptocarpa, C. ramenskii,* and *Potentilla pacifica.* Most of these species are widely distributed in this type of habitat in Alaska, and elsewhere in the Arctic and Subarctic. Polunin

(1948) discussed the invasion of silty seashores by these or similar species on the west coast of Hudson Bay, Ellesmere Island, and in other parts of the eastern Canadian Arctic; Cooper (1931) on the shores of Glacier Bay in southeastern Alaska; Oosting (1948) in East Greenland; Westhoff (1947) in the Dutch Islands, Terschelling, Vliland, & Texel; Iverson (1936) and others in Denmark; Braun-Blanquet (1932) in the Europeo-Mediterranean salt-marsh communities, and others.

The communities are arranged below in sequence from the lowest, wettest, and most saline substratum to the highest, driest, and least saline. The most complete series of stages was found on the Goose Bay estuary on the north side of Knik Arm. Sequence of communities: 1) *Puccinellia phryganodes-Salicornea herbacea-Suaeda maritima,* 2) *Plantago juncoides-Puccinellia triflora-P. glabra,* (Stand 15), 3) *Triglochin maritima-Potentilla pacifica* (Stand 57), 4) *Carex ramenskii-Triglochin maritima-Potentilla pacifica* (Stand 58), 5) *Carex pluriflora-C. cryptocarpa* (Stand 59), 6) *Carex cryptocarpa* (Stands 41, 6, 26A, 7) *Carex cryptocarpa-Calamagrostis canadensis* (Stands 26B, 11), 8) *Calamagrostis canadensis-Myrica gale,* 9) *Calamagrostis canadensis-Deschampsia beringensis-Juncus balticus-Festuca rubra* (Stands 12, 13), and 10) meadow types such as Stands 32, 39 and 40 with *Festuca rubra, F. altaica Poa palustris, Agropyron trachycaulum,* and forbs. Willows and alders (Stand 25) may invade a number of these communities from 7 on, and cottonwood forest (Stand 8) may invade in time. Several of these communities may not appear in the zonation in a particular area because of the influence of factors such as the degree of slope, the rate of silt deposition, drainage, etc. The zonation is altered where the land near the water's edge is better drained and has a firmer surface than farther inland, as on the eastern part of the Goose Bay estuary, and on the shores at Homer and east of Anchorage. According to Imanishi (1950), large areas on wide valley floors and middle reaches of the Gan and Albazikha rivers in northwestern Manchuria occupied by reed semi-swamp are dominated by *Calamagrostis langsdorfii.* This type resembles communities in Alaska in which *C. canadensis* is the chief dominant.

SEQUENCE OF COMMUNITIES ON LOWLANDS IN THE VICINITY OF KOTZEBUE

Kotzebue is situated on the northwestern tip of Baldwin Peninsula, which separates Kotzebue Sound from Hotham Inlet, in northwestern Alaska, latitude about 67° N., longitude 162° 40′ W. of Greenwich. A long series of beach bars, or a spit, extends along the northwestern shore of Baldwin Peninsula from one headland northeastward toward another headland, almost enclosing a small bay. The spit is made up of low, broad ridges, and marshy land, the latter mostly on the nearly land-locked bay side. Smith and Mertie (1930, p. 238) described the action of the ice in building up beaches as follows "—one of the processes which in northern Alaska has been largely instrumental in eroding material from the sea floor and heaping it up in the ridges that form the reefs is the sea ice. Each year the young ice that forms on the sea to the depth of 5 feet or less becomes attached to the material of the sea floor where the water is shallow, and the thicker ice of the pack, which may be tens of feet thick, is driven against the material resting on the sea floor. Thus by floating and rasping they bring shoreward considerable quantities of detritus, which serves to renew the seaward faces of the beaches and cover many of them with coarse material entirely dissimilar from the smaller material usually handled by the water currents."

The vegetation on the marshy land varied considerably, from brackish sedge-marsh adjoining the inlets and ponds which are subject to overflow during storms and for several days thereafter (Stands 72, 69), fresh water sedge-marshes (Stand 70), sedge-heath hummocky, mosaic-type communities (Stands 71, 73), and gravelly low ridges between marshy areas (Stand 74). During storms the waves and wind raise the level of water along the beach facing Kotzebue Sound and the water is backed up into the bay and ponds and on the lower marsh land, where it may remain for several days before slowly returning to usual levels.

STAND 72 CAREX SUBSPATHACEA

This community formed a zone in the saturated borders of brackish pools and ponds. It was subject to overflow by water backed up by storms. *Carex subspathacea* formed almost a pure stand in the shallow water, and *Hippuris vulgaris* formed an open growth in the deeper water. On the wet borders of the pools in which this stand was studied on August 15, 1949, *C. subspathacea* was very dense, accounting for 80% of the high degree of cover, 1690 points. Only ten species occurred. *Carex glareosa* and *Potentilla pacifica* were intermediate in cover and in frequency (see Table 3). While *Elymus mollis* and *Poa eminens* did grow in this stand they were more abundant on sandy shores.

The soil profile consisted of peat, very dusky red to reddish brown to a depth of 21 inches; compact fine silt at 21-32 inches; partly decomposed plant debris mixed with silt at 32-36 inches; and below 36 inches a small amount of gravel mixed with silt and plant debris. The maximum depth of the roots was only 21 inches. No frozen ground was encountered to slightly below 36 inches, as deep as dug.

STAND 69 CAREX RARIFLORA

This stand, studied on August 10, 1949, was situated on slightly higher land than the preceding stand and was not subject to flooding by brackish water for as long a time following storms. Low hummocks, 4 to 12 inches high, 0.5 to 3 feet broad, and up to 6 feet long, were scattered over the general level of the marsh. The general level, or "depressions," was occupied chiefly by sedges, especially *Carex rariflora,* which constituted about 52% of the total cover. *C.*

TABLE 3. Communities on Lowlands in the Vicinity of Kotzebue.

Species	Stand 72		Stand 69		Stand 70		Stand 71	
	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %
Carex subspathacea	1395	100	3	5				
Carex glareosa	119	75	66	55				
Carex rariflora			374	90	x			
Carex aquatilis					295	100		
Carex rotundata					205	95		
Carex livida					40	60		
Carex capillaris					1	5		
Carex bigelowii							30	42
Carex nesophila					50	30		
Carex sp.							2	5
Carex atrofusca					x			
Carex physocarpa					x			
Carex bicolor					x			
Eriophorum angustifolium					18	35		
Eriophorum chamissonis					3	10		
Scirpus caespitosus callosus					x			
Calamagrostis deschampsioides	20	45	15	10				
Elymus mollis	21	40	9	20				
Puccinellia borealis	11	20						
Deschampsia caespitosa			31	25				
Festuca rubra			16	25				
Dupontia fisheri			13	5				
Poa eminens	28	50						
Potentilla pacifica	108	100	x					
Stellaria humifusa	34	60	x					
Chrysanthemum arcticum	4	15	13	35				
Pedicularis sudetica	x		x		13	30		
Pedicularis pennellii					x			
Saussurea subsinuata			38	55				
Androsace chamaejasme			10	20				
Primula sp.			3	10				
Montia laprosperma			2	5				
Parnassia palustris			x					
Lomatogonium rotatum			x					
Castilleja sp.			x					
Tofieldia coccinea							x	
Salix ovalifolia			111	85				
Salix fuscesens reducta					19	30		
Salix richardsonii					x			
Betula nana exilis					x		36	25
Rubus chamaemorus					x		40	75
Empetrum nigrum			10	10			30	40
Andromeda polifolia					1	5		
Ledum decumbens							177	95
Vaccinium vitisidea							127	95
Vaccinium uliginosum							66	50
Arctostaphylos alpina							49	65
Hypnaceae spp.					200	100		
Dicranum sp.							16	30
Polytrichum sp.							14	45
Sphagnum sp.							1	5
Cetraria cucullata							91	95
Cetraria islandica							40	80
Cetraria tilesii							1	5
Alectoria nigricans							59	65
Alectoria ochroleuca							13	30
Cladonia rangiferina							20	60
Cladonia amaurocraea							16	45
Cladonia sp.							37	80
Thamnolia vermicularis							7	30
Sphaerophorus sp.							6	15
Baeomyces sp.							1	5
No hits			10				1	
Total number of hits	1690		714		845		891	

glareosa was more scattered and *C. subspathacea* was scarce. The most common species on the hummocks were *Salix ovalifolia, Festuca rubra, Empetrum nigrum,* and *Calamagrostis deschampsioides.* The slight differences in elevation brought about by the hummocks altered the habitat considerably with regard to exposure to winds and sunlight, water content and aeration of the substratum, duration of standing water, salinity, depth to the frozen ground (nearer the surface in the hummocks due to the insulating effect of vegetation on them), and to the heat-absorbing capacity of the water in the depressions. The soil profile descriptions below show the irregularities in the soil horizons in the hummocks compared to the regularity in the depressions. These variations within short distances cause the development of a mosaic of microcommunities. Hanson (1950b) described additional features of this area.

Detailed description of the soil profile in a depression:

Sedge leaves extended 4 to 6 inches above a 2-inch layer of dead leaves and stems, with scattered moss.

0-1.25 inches. Dark reddish brown mucky organic material, very little silt, somewhat fibrous, picks out in soft irregular aggregates, saturated, rhizomes frequent, roots very abundant.

1.25-2 inches. Similar to above but yellowish red.

2-4 inches. Dark gray brown, silt, much organic matter and some sand, rather fibrous, picks out in soft aggregates, containing many roots, saturated.

4-9 inches. Very dark gray, mostly partly decayed plant material, little silt, fibrous, picks out in soft blocks, saturated, many dead roots and very many live roots.

9-10.5 inches. Dark reddish brown, peat, saturated, small stones scattered in lower part, roots numerous.

10.5-12.25 inches. Dark gray brown, peat, small amount of silt, picks out in soft aggregates, numerous fine roots.

12.25-14 inches. Very dusky red, peat, mostly well decomposed pieces of plants, moderate amount of silt, occasional gravel particles, saturated, roots few.

14-15 inches. Gravel, silt to fine sandy silt, gray, ground frozen at 15 inches, roots scarce, working depth at 11.5 inches, maximum 15 inches.

Detailed description of the profile in a hummock 6 inches high, adjacent to above profile:

Foliage reached average height of 4 to 5 inches above the 2-inch layer of dead leaves, stems, and scattered moss. Ground was frozen at 20 inches. Horizons were irregular due to frost action. The top horizon, varying from 2 to 3 inches on the summit to 3 to 5 inches on the sides, consisted of dark reddish brown mostly decomposed plant remains. A peat layer, about 5 inches thick, consisting mostly of short partly decomposed pieces of plants, similar to the 9-10.5-inch horizon in the depression, extended diagonally from the frozen ground into the middle of the hummock and to within 3 to 5 inches of the surface. Below the peat was gravelly silt. Other hummocks in this vicinity had a thinner layer of peat and the frozen ground was closer to the surface. The higher hummocks and mounds had taller and denser growth of heath plants.

STAND 70 CAREX AQUATILIS-C. ROTUNDATA

This stand, studied on August 11, 1949, was located in one of the larger, basin-like areas that at one time had probably been a brackish pond subject to overflow from storm waters, then a fresh water pool or brackish marsh similar to Stand 72, and finally, as the elevation increased, a fresh water marsh surrounded by still higher land occupied mainly by heath plants, lichens, and scattered sedges. As shown in Table 3, 9 species of *Carex*, 2 of *Eriophorum*, and 1 of *Scirpus* were noted in a total of 19 vascular species. *Carex aquatilis* and *C. rotundata* made up about 60% of the cover, mosses nearly 24%. The foliage was generally 12 to 15 inches high, and a few Carex spikes reached 24 inches. The conspicuous white inflorescences of *Eriphorum angustifolium* and *E. chamissonis* made these species appear more important than the cover and frequency data justified. Species characteristic of higher land were found as pioneer invaders in this stand, such as *Salix fuscesens reducta, S. richardsonii, Pedicularis sudetica, Andromeda polifolia,* and *Pedicularis pennellii.*

Important features of the soil profile were 1) frozen ground at 22 inches, 2) beneath a 2-inch layer of plant debris and moss was a 15.5-inch layer of peat underlaid by rather impervious silt to 17.25 inches, and then gravel, 3) water level at 6 inches, 4) rapid diminution in number of roots below the working depth at 18.25 inches.

STAND 71 LEDUM DECUMBENS-VACCINIUM VITISIDEA-CETRARIA SPP.

This heath-lichen stand, studied on August 11, 1949, was located on areas 1 to 2 feet higher than the fresh water sedge marsh (Stand 70). These slightly elevated areas were in the form of mounds or ridges, up to a rod or two in width and several rods long, forming an irregular network surrounding fresh water marsh. The chief species in Stand 71 were *Ledum decumbens* and *Vaccinium vitisidea.* On the more exposed and open spots many lichen species were growing, most of the cover contributed by *Cetraria cucullata, C. islandica,* and *Alectoria nigricans* (see Table 3). A total of 23 species, including mosses and lichens, were found in this stand. The total cover was rather low, 891 hits. The fruits of *Vaccinium uliginosum* and *Rubus chamaemorus* were ripe and were gathered by Eskimoes, especially women and children, on the more pleasant days. The sedges were conspicuous as the leaves were 4 to 6 inches and the inflorescences 8 to 9 inches above the trailing stems of Ledum and Vaccinium. This stand shows resemblance to Nordhagen's (1943) Association *Oxycoccus microcarpus-Empetrum hermaphroditum-Cladonia* spp. in the dwarf shrub bog order (*Oxycocco-Ledetalia palustris*). The formation of some of the mounds and hummocks and the plant succession closely resemble these processes in Norway as described by Nordhagen (1943). Freely translated, he stated:

When *Sphagnum fuscum* hummocks reach a certain height they become drier, the protecting winter snow-cover becomes thinner the higher the hummocks become. Sphagnum loses vigor, and the hygrophilous nature of the flora diminishes or disappears. Dry substratum species appear on the dead Sphagnum cushions, especially *Vaccinium vitisidea*, mosses in the genera *Dicranum, Pleurozium,* and *Hylocomium,* and a number of lichens, especially Cetraria and Cladonia, as well as crustose species. If snow cover is good, mosses take over, if the wind has great force and blows the snow away in the winter, lichens become dominant.

The ground was covered with a 2.5-inch layer of lichens, moss, and other plants. The soil to a depth of 3 inches was partly decomposed organic material with a small amount of silt. At 3-5.5 inches it was black, with more silt, and below that to 10.5 inches, where the ground was frozen it was silt. Seepage occurred at 5 inches and roots were numerous to the frozen ground. Frost action was indicated by the silt masses in the upper horizons.

STAND 74 DRYAS INTEGRIFOLIA-LICHENS

This stand, studied on August 11, 1949, and again in July, 1950, was located on one of the low, raised beaches, 60 to 75 feet wide, between marsh and heath communities on the Kotzebue spit. These ridges consist largely of gravel. The surface had a barren appearance because the lichens which formed most of the cover were short, varying from a thin crust of foliose species to a layer of fruticose species 1 to 2 inches high. In spots protected from the wind, as in slight depressions under dwarf shrubs, the lichens were 2 to 2.5 inches high. Scattered plants of the following were observed; *Empetrum nigrum, Vaccinium uliginosum, Arctostaphylos alpina, Carex* sp., *Hierochloa alpina, Pedicularis lanata, Epilobium latifolium,* and *Ledum decumbens.* Low mounds, built by tussocks of plants, were scattered in places. In some areas the cover was greater and additional species were noted, such as *Saxifraga tricuspidata, Dryas integrifolia,* both very abundant in places, *Poa sp., Astragalus* sp., *Salix reticulata, Salix* sp., *Betula nana exilis, Vaccinium vitisidea.*

Important features of the soil profile were 1) the thin cover consisting mostly of lichens, 2) the very dark silt loam and gravel to 10 inches, and the brown gravel, darkened presumably by organic matter to 18 inches, 3) no frozen ground as deep as dug, 28 inches, 4) roots numerous at 0-5 inches, and at 15-16 inches, working depth at 16 inches, maximum at 17 inches.

DISCUSSION OF THE SEQUENCE OF COMMUNITIES ON LOWLANDS IN THE VICINITY OF KOTZEBUE

The various plant communities appear more often in mosaic patterns on the lowlands in the vicinity of Kotzebue, rather than as more or less elongated zones on the estuaries and coasts of Kodiak and the Cook Inlet Region. This is due to several causes such as the presence of numerous ponds and other poorly drained areas, the shallowness of the frozen ground, and frost action in the Kotzebue Region.

On low areas adjacent to inlets, channels, and ponds, covered with shallow, brackish water, or subject to overflow during storms (Stand 72), the most abundant species was *Carex subspathacea.* In this vicinity it takes the place of *Carex cryptocarpa* which occurs in similar habitats in south central Alaska. On the estuaries in the vicinity of Nome both species occur. Other characteristic species in this habitat near Kotzebue were *Puccinellia borealis, Potentilla pacifica,* and *Stellaria humifusa.* The 2 latter were also prominent in south central Alaska. The peat substratum, 21 inches thick, was underlaid by silt and gravel. Permafrost was not encountered to a depth of 3 feet (as deep as dug), due evidently to the warming effect of the water.

On higher land, less subject to inundation by brackish water (Stand 69), *Carex rariflora* and *C. glareosa* replaced *C. subspathacea* to a large extent. The second of these occurred in the sequence in south central Alaska, but not the first. *Deschampsia caespitosa, Dupontia fisheri, Saussurea subsinuata,* and *Chrysanthemum arcticum* were more numerous than in the more saline areas. Species evidently less tolerant of salinity and saturated soil such as *Salix ovalifolia, Festuca rubra, Calamagrostis dechampsioides,* and *Empetrum nigrum* occurred on low hummocks about 6 inches high. The ground was frozen at 15 to 20 inches, or less; usually at a shallower depth under the hummocks than in the depressions.

As the hummocks increase in height and diameter, due to the accumulation of plant materials and to the effects of frost action (Bryan 1946, Hopkins & Sigafoos 1950), a mosaic pattern is formed in which dwarf heath shrubs, lichens, and mosses become more numerous and finally become dominant (Stand 71). This succession of microcommunities is discussed in more detail by Nordhagen (1943, p. 533) and Hanson (1950b).

On low, wet areas, not inundated by brackish water, and with frozen ground at about 20 inches, various species of *Carex,* especially *C. aquatilis, C. rotundata,* and *Eriophorum* formed a fairly uniform cover, with a carpet of moss on the ground (Stand 70). As hummocks, mounds, and tussocks are formed grasses, dwarf heath shrubs, lichens, and forbs invade; resulting finally in a heath-lichen community (e.g. Stand 71), with frozen ground near the surface.

Many species grow on the barren, firm, gravelly broad ridges, apparently raised beaches (Stand 74), common on the low shores of Kotzebue Sound. The cover was often dense but the plants were short. Some of the most numerous and characteristic plants were the dwarf heath shrubs, usually with decumbent stems, short lichens which may reach about 2.5 inches in protected spots, *Saxifraga tricuspidata, Dryas integrifolia,* and dwarf *Salix* spp.

On gravelly and sandy beaches and dunes, communities, similar to those in south central Alaska, are formed by *Arenaria peploides, Mertensia maritima, Elymus mollis, Lathyrus maritimus, Poa eminens,* and associated species.

GRASSLAND COMMUNITIES ON UPLANDS

The grassland stands that were studied on the uplands have been classified into the following groups: 1) "Cliff Meadow," consisting of many kinds of grasses and forbs, found above cliffs on seashores of Kodiak Island; 2) Tall Grass-Forb Communities, with *Calamagrostis canadensis* as the chief dominant; 3) Medium Tall Grass-Forb Communities with *Festuca altaica* as the chief dominant; 4) Medium Tall Grass-Forb Communities with *Agropyron trachycaulum* as the chief dominant; 5) Miscellaneous Communities with various species of grasses as dominants, occurring at higher elevations and nearer the interior of Alaska than most of those in the first 4 groups. Similarities within and between these 5 groups can be seen by comparing the analyses of the stands as given in the tables. Similarities and differences in the vegetation and in soils are treated in the section on Discussion of Grassland Communities on Uplands.

CLIFF MEADOW COMMUNITIES

Only two examples, both on Kodiak Island, of this well developed community were studied. They occurred near the edge of cliffs and apparently represent a widespread community on the top of cliffs bordering the sea. These two examples were the richest in species and the best developed stands that were studied during 1949. The large number of species and the well developed profiles were associated with the proximity of the cliff edge, the shallowness of the ash deposit, and with the age of the stand. Species from the face of the cliff, from nearby grasslands, and from higher elevations, found favorable conditions here for association.

STAND 1 DESCHAMPSIA BERINGENSIS-FORBS

This stand of grasses and forbs, studied on June 20, 1949, was on a south-southwest slope, about 2 rods inland from the edge of the rocky cliff on Miller's Point, northeast of the town of Kodiak. The slope varied from 5 to 15°. In places the slope was parallel to the edge of the cliff, in other places at right angles. Inland a few rods this stand was bordered by grassland and then by dense Sitka spruce forest. The spruce was having considerable difficulty in invading due, partly to the competition of the spruce seedlings with the established grasses and forbs, and partly to the wind in this exposed situation. Some of the young trees that had managed to grow a few feet high were deformed and some had died. The Katmai ash deposit was only about an inch thick, the rest having been blown or washed away shortly after deposition In depressions farther down the slope the ash was 11.5 inches deep. There was no indication that the area had been burned over.

At least 47 vascular species (34 hit), and several kinds of mosses and lichens were found. The cover

was fairly good, 1117 hits, of which 42% was *Deschampsia beringensis.* Mosses also furnished much cover. Other important species, as shown in Table 4, were *Festuca rubra, Carex macrochaeta, Angelica lucida, Geranium erianthum,* and *Achillea borealis.* Five additional grasses, *Poa glauca, Calamagrostis canadensis, Phleum alpinum, Hierochloe odorata,* and *Trisetum spicatum* were found, making a total of 7 grasses and 1 sedge. A characteristic of this stand was the large number of species with sparse distribution, 28 of the 47 species were hit only once or twice, or merely observed in the stand. This community, then, was composed in large measure of a few individuals of many different species, in contrast to many of the preceding and following communities in which the individual plants belonged to a much smaller number of species.

Down slope from this stand *Calamagrostis canadensis, Hierochloa odorata, Angelica lucida, Heracleum lanatum,* and *Athyrium filix-femina* were more abundant, and other species, especially forbs, had disappeared, more straw had accumulated, and the growth was taller. On the flat area near the bottom of the slope *Calamagrostis canadensis* formed almost a pure stand.

Outstanding features of the soil profile were 1) excellent drainage to bedrock, 2) very thin ash layer, 3) large number of roots to 14 inches, working depth at 19 inches, maximum 35 inches, 4) the deep fertile soil to depth of 33 inches, excellent structure for root growth, 5) decomposing argillite and shale rocks below 33 inches, 6) pH 6.6 in the ash layer, pH 4.8 to 5.2 below the ash.

STAND 18 POA GLAUCA-CAREX MACROCHAETA-CALAMAGROSTIS CANADENSIS-FORBS

This stand, studied on June 18, 1949, was located on a 30- to 50-foot wide strip along the margin of a cliff about 50 feet high on Isthmus Bay Point, Kodiak Island (Fig. 16). The land sloped gently toward the west, away from the cliff edge, at about 5 to 10°. Lower down the slope fewer species of forbs occurred (see Stand 16). This is an old stand, very similar to the preceding and others on cliff margins on Kodiak Island. The roots and rhizomes held together the surface foot or so of soil so firmly that when underlying rocks fall away the sod forms a mantle over the edge. These mantled cliffs are characteristic of Kodiak Island. The cover was greater than in the preceding stand, 1262 points. The 3 grasses named in the heading made up about 33% of the cover and 4 additional grass species occurred; *Festuca rubra, Deschampsia beringensis, Poa* sp., and *Elymus mollis.* The total number of vascular species was 36. In total number and kinds of species and in frequency there was much similarity to Stand 1, as shown in Table 4. Forbs high in frequency and cover were *Angelica lucida, Dodecatheon macrocarpum, Achillea borealis,* and *Viola adunca.*

Outstanding features of the soil profile were 1) the large quantity of organic material to below 17 inches, 2) ash layer only 0.75 inch thick, 3) presence of apparently earlier ash deposits at 22.75-27.25 and 31.25-41.25 inches, 4) acid reaction, pH 5.4 to 6.8, 5) roots

TABLE 4. Cliff Meadow Communities on Kodiak Island.

Species	Stand 1		Stand 18	
	Hits	Freq. %	Hits	Freq. %
Deschampsia beringensis	459	100	40	25
Poa glauca	26	50	192	65
Carex macrochaeta	92	75	127	65
Festuca rubra	70	85	73	50
Calamagrostis canadensis	21	20	105	70
Phleum alpinum	2	5		
Elymus mollis	..	..	25	30
Poa sp.	..	..	42	15
Hierochloe odorata	x			
Trisetum spicatum	x			
Luzula multiflora	3	15	12	15
Angelica lucida	42	60	106	80
Dodecatheon macrocarpum	17	45	74	70
Geranium erianthum	33	70	46	40
Achillea borealis	33	75	28	85
Viola adunca	..	..	22	60
Viola langsdorfii	12	35		
Fritillaria camtchatcensis	11	30	19	45
Lupinus nootkatensis	9	20	20	35
Cornus suecica	29	40		
Iris setosa	15	25	15	15
Galium boreale	13	20	7	15
Trientalis europaea arctica	10	35	3	15
Castilleja unalaschkensis	6	10	2	10
Sanguisorba sitchensis	11	30		
Arenaria lateriflora	5	10	2	5
Solidago sp.	4	10		
Solidago multiradiata	..	..	8	15
Equisetum arvense	2	10	8	15
Equisetum scirpoides	..	..	1	5
Equisetum sp.	x			
Rhinanthus borealis	2	10	7	20
Cypripedium guttatum	2	10	7	15
Campanula rotundifolia	4	5	4	20
Polygonum viviparum	1	5		
Stellaria sp.	1	5		
Heracleum lanatum	3	5	5	20
Lathyrus pratensis	1	5	8	25
Orchis aristata	1	5	4	20
Epilobium angustifolium	1	5	36	30
Potentilla villosa	x			
Dryopteris disjuncta	x			
Conioselinum benthami	x		2	10
Anemone narcissiflora	x			
Parnassia palustris	x		6	15
Geum calthifolium	x			
Veratrum eschscholtzia	x			
Aconitum delphinifolium	..	..	6	25
Prenanthes sp.	..	..	2	5
Pedicularis verticillata	..	..	2	5
Arnica sp.	x			
Seedling	1	5	1	5
Salix sp.	18	20		
Rubus stellatus	1	5	15	25
Picea sitchensis	x			
Arctostaphylos alpina ?	x			
Hypnaceae spp.	142	80	179	100
Polytrichum sp.	14	10		
Cladonia sp.	x			
Peltigera sp.	x			
No hits	1			
Total number of hits	1117		1262	

FIG. 16. Cliff meadow community, *Poa glauca-Carex macrochaeta-Calamagrostis canadensis*-Forbs (Stand 18) on Isthmus Bay Point, Kodiak Island, June 18, 1949.

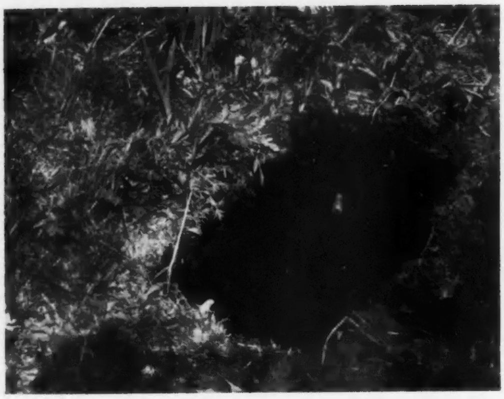

FIG. 17. Soil profile in a cliff meadow community (Stand 18, see Fig. 16) with only a thin ash layer between 1 and 1.75 inches; an old stand on deep, well drained, fertile soil. See Table 4. Isthmus Bay Point, Kodiak Island, June 18, 1949.

numerous to working depth at 16 inches, maximum at about 41 inches.

Detailed description of the soil profile:

In digging the trench the soil was cut into chunks about a foot square and about a foot deep and lifted out intact. The ash layer at 1 inch had a slight separating effect. The surface was covered usually with a layer of moss up to 0.5 inch thick.

0-1 inch. Dense fibrous mass of roots and rhizomes with very little mucky material and scattered light gray ash grains, pH 6.6.

1-1.75 inches. Gray ash, single grain, numerous finely branched roots, no effervescence with 10% HCl, pH 6.8.

1.75-9.25 inches. Very dark brown mucky material with slate fragments up to 1 inch long which crumble readily, little structural development, moist, roots very numerous in upper part but decrease rapidly in lower part, no effervescence, pH 5.8.

9.25-16.75 inches. Dark brown mucky material similar to horizon above but sharp-edged slate and argillite fragments increase with depth, more silt in lower part, weak structure, roots numerous to working depth at 16 inches, no effervescence, pH 5.6.

16.75-22.75 inches. Dark brown to yellowish red, silt loam, numerous slate and argillite fragments, much organic material, moist, roots few, no effervescence, pH 5.6.

22.75-27.25 inches. Yellowish red, silt loam, gritty, reddish yellow streaks along old root channels, pinholes frequent, probably an older ash deposit, roots few, no effervescence, pH 5.4.

27.25-31.25 inches. Reddish gray, apparently clay loam, very small slate fragments scattered, roots very few, pH 5.6.

31.25-41.25 inches. Similar to 22.75-27.25-inch layer but more variable in color and containing rocks up to 6 inches through, roots scarce.

41.25-44 inches. Dark gray, sandy loam with many rock fragments, wet, roots scarce to maximum depth at 41.25 inches.

TALL GRASS-FORB COMMUNITIES WITH CALAMAGROSTIS CANADENSIS AS THE CHIEF DOMINANT

A number of stands (Table 5), characterized by the dominance of *Calamagrostis canadensis* and the presence of several species of tall forbs, were studied in detail on Kodiak Island, on the uplands near Homer, and in the vicinity of Palmer and in the Talkeetna Mountains. Some of the most common forbs were *Epilobium angustifolium, Heracleum lanatum, Geranium erianthum,* and *Sanguisorba sitchensis.* These communities resemble Nordhagen's associations in Norway in the Tall Herb Meadow Order in the Mountains (*Aconitetalia*), a widespread order in Scandinavia and central Europe (1943). In Norway, as in Alaska, these communities are widespread in the open or as a ground layer in open forest, from sea-level to the low alpine region. Nordhagen states that these communities have probably existed in Norway for thousands of years without much change except in the tree or shrub layer. They furnish much feed for livestock.

STAND 16 CALAMAGROSTIS CANADENSIS-FORBS

This stand was on the lower side of Stand 18, "cliff-meadow," away from the cliff, on Isthmus Bay Point, Kodiak Island. It was part of a zone about 2 rods wide on a west-facing 5°-10° slope. It was intermediate in elevation and in number of species to Stand 18 and Stand 17, a *Calamagrostis canadensis* community lower on the slope. Stand 16 was a pronounced tall grass-tall forb type with *Calamagrostis canadensis, Angelica lucida,* and *Heracleum lanatum,* especially conspicuous at the time of study on June 28, 1949. *Calamagrostis canadensis, Deschampsia beringensis, Carex macrochaeta, Festuca rubra,* and *Elymus mollis* made up 62% of the plant cover which totalled 1382 hits. *C. canadensis* alone occupied 35% of the cover. The total number of vascular species was 33, of which 24 were hit (Table 5).

Outstanding features of the soil profile were 1) the tap roots of *Heracleum lanatum* extended to the depth of 16 inches where they were still 0.5 inch in diameter and where branching to horizontal laterals occurred, 2) working depth of roots at 25 inches, maximum 44.25 inches, 3) apparently 3 ash layers, at 1.75-7.25

TABLE 5. Tall grass-Forbs Communities with *Calamagrostis canadensis* as the Chief Dominant.

Species	Stand 16 Kodiak		Stand 17 Kodiak		Stand 24 Kodiak		Stand 43 Lazy Mt.		Stand 49 Susitna C.		Stand 51 Talk. Mts.		Stand 56 Talk. Mts.	
	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %
Calamagrostis canadensis	484	95	822	100	544	100	836	100	407	95	146	90	147	80
Festuca rubra	83	30			10	5								
Festuca altaica	x										x		130	35
Poa palustris									11	10				
Poa glauca	x										19	20		
Poa arctica													43	55
Poa sp.											1	5		
Deschampsia beringensis	156	50												
Elymus mollis	23	40												
Phleum alpinum											18	30	21	45
Carex macrochaeta	112	30												
Carex mertensii											21	5		
Carex brunnescens											6	5		
Carex sp.													21	5
Luzula multiflora	x												2	5
Epilobium angustifolium	21	50	24	30	53	65	48	60	54	80	34	60	53	50
Heracleum lanatum	27	25			9	15	x		4	20	7	15	x	
Achillea borealis	29	50											7	10
Equisetum arvense			34	35	95	65	27	20						
Equisetum sylvaticum							568	90	32	25				
Equisetum pratense									2	5				
Equisetum sp.	9	15												
Geranium erianthum	x				6	5			1	5	88	75	124	85
Angelica lucida	100	65	1	5										
Angelica genuflexa					116	90								
Castilleja unalaschkensis	10	5									8	15	15	25
Mertensia paniculata									30	45	9	25	59	40
Arenaria lateriflora					9	20			9	25	14	30	30	40
Lupinus nootkatensis	7	5												
Sanguisorba sitchensis					4	20					82	55	139	80
Aconitum delphinifolium											9	20	8	10
Veratrum eschscholtzia											15	30	1	5
Streptopus amplexifolius									x		5	5	4	15
Trientalis europaea arctica	3	5	7	25	1	5	3	5	15	30	24	40	13	35
Conioselinum benthami	1	5			1	5								
Lathyrus palustris	19	35			5	5								
Lathyrus maritima			4	10										
Galium boreale	18	15												
Galium triflorum									16	10	7	20	6	15
Viola langsdorfii	13	20												
Viola adunca											14	30	7	15
Solidago ?	36	20			82	45								
Arnica sp.	9	25												
Dodecatheon macrocarpum	7	15												
Ligusticum hulteni	5	5												
Stellaria calycantha									12	15	4	10		
Stellaria sp.	1	5												
Fritillaria camtchatcensis	1	5									x		x	
Rhinanthus borealis	1	5												
Aquilegia formosa											64	20	x	
Athyrium filix-femina					31	30					249	85	157	35
*Dryopteris austriaca**														
Dryopteris disjuncta							x		136	95	46	40	123	95
Dryopteris oreopteris									x					
Dryopteris phegoptera													18	15
Botrychium boreale													1	5
Botrychium lunaria											2	10		
Lycopodium annotinum													34	25
Orchis aristata	x													
Limnorchis dilitata	x													
Parnassia palustris	x													
Iris setosa	x													
Cardamine umbellata			1	5	3	10								
Claytonia sibirica					6	10								
Corydalis pauciflora									2	10				
Artemisia arctica													26	10
Arabis lyrata									x					
Actaea spicata									x					

TABLE 5—Continued

Species	Stand 16 Kodiak		Stand 17 Kodiak		Stand 24 Kodiak		Stand 43 Lazy Mt.		Stand 49 Susitna C.		Stand 51 Talk. Mts.		Stand 56 Talk. Mts.	
	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %
Cornus canadensis									x				120	75
Draba glabella											15	30	10	25
Senecio triangularis											1	5	2	10
Valeriana sitchensis											x		210	75
Gentiana propinqua													6	10
Smilacina stellata													x	
Sedum roseum													x	
Seedling	7	30												
Rubus spectabilis					72	50								
Rubus strigosus									15	10				
Rubus stellatus									x				23	45
Rubus sp.											3	10		
Sambucus racemosa pubens							x							
Rosa acicularis			x						5	10				
Spiraea beauverdiana													x	
Viburnum edule									x					
Empetrum nigrum													26	10
Vaccinium caespitosum													56	25
Hypnaceae spp.	200	100	200	100	195	100	50	25	x		93	80	144	100
No hits							1		7		8			
Total number of hits	1382		1093		1242		1532		751		1004		1786	

* Included in the count with *Athyrium filix-femina* in Stand 51.

inches, 23.75-27.75, and 36-38 inches, separated by silt loam containing slate or argillite fragments, 4) deep fertile soil, well drained, to argillite rock at 46.25 inches, 5) an old stand as indicated by the profile.

STAND 20 DESCHAMPSIA BERINGENSIS

This stand was situated on the south-facing slope (about 15°) of a small hill on the border of the Kalsin Bay estuary, Kodiak Island. It was examined on July 1, 1949. It appeared to be a transitional stage in succession between the *Deschampsia beringensis*-Forbs, "cliff meadow" community (Stand 1) and the preceding *Calamagrostis canadensis*-Forbs community. It resembled the former in that *D. beringensis* was the chief dominant; it resembled the latter in having a smaller number of species than Stand 1, and that most of these were tall forbs. It also had considerable *C. canadensis* and moss. Other leading species were *Luzula multiflora, Epilobium angustifolium,* and *Angelica lucida.* Additional species were *Castilleja unalaschkensis, Achillea borealis, Equisetum arvense, Galium boreale,* and *Festuca rubra.*

This site appeared infertile. *Calamagrostis canadensis* was invading and beginning to offer much competition to *Deschampsia.* Other factors in this site were the excellent drainage, the southfacing slope, the thick ash deposit at 1.5-12 inches beneath the 0-1.5-inch organic loam layer, and the underlying mucky material with scattered rocks at 15 inches and below.

STAND 17 CALAMAGROSTIS CANADENSIS

This stand was adjacent to Stand 16 and slightly lower on the same west-facing slope (about 15°) on Isthmus Bay Point. On the landward side it was bordered by Sitka spruce forest. It differed greatly from Stand 16 in that the cover was almost exclusively *Calamagrostis canadensis* and fewer species of forbs. On June 30, 1949, *C. canadensis,* 2.5-3 feet tall and beginning to head, made up 822 of the total of 1093 hits; mosses made up 200 hits (Table 5). The most conspicuous tall forbs were *Epilobium angustifolium* and *Equisetum arvense.* There were only 9 vascular species.

Outstanding features of the soil profile were 1) the greater maturity of this profile compared to the similar one in Stand 16, with less stone and gravel below the ash, 2) the 0-2-inch organic horizon, beneath a loose 6-inch layer of straw, indicated rapid development since 1912, 3) ash layers at 2-15 inches, 4) well developed silt and sandy silt horizons, with scattered rocks, below the ash to 41 inches, where gravel was found, 5) deep penetration of the roots, working depth at 23 inches, maximum about 49 inches.

STAND 24 CALAMAGROSTIS CANADENSIS-ANGELICA GENUFLEXA-FORBS

This stand was representative of the tall grass-forb vegetation covering extensive areas between the shrub thickets on the lower parts of hillsides bordering Kalsin Bay, Middle Bay, and elsewhere on Kodiak Island. It was situated on a slope of about 15°, facing southeast, on the northwest side of Kalsin Bay, and was studied on June 24, 1949. The vegetation was dense, but the cover index of 1242 points was only moderately high. *Calamagrostis canadensis,* 3 to 5 feet high, with flowering stalks of the pre-

vious year still upright, made up about 42% of the cover (Fig. 18). Other prominent species in the total of 17 vascular species were *Angelica genuflexa, Rubus spectabilis, Equisetum arvense*, and *Epilobium angustifolium* (see Table 5).

Important features of the soil profile were 1) the large quantity of straw on the surface and the densely fibrous 0-1-inch horizon, 2) the stratified 1-11.25-inch ash layer, apparently undergoing fairly rapid change, 3) the thick organic horizons between 11.25 and 20.5 inches, indicating an old stand, probably similar to the present one, 4) excellent root development, working depth at 31.75 inches, 5) soil reaction pH 5.0-5.6, 6) clay forming from argillite rocks (Fig. 19)

FIG. 18. *Calamagrostis canadensis-Angelica genuflexa*-Forbs community on the northwest side of Kalsin Bay, Kodiak Island, June 24, 1949. Stand 24.

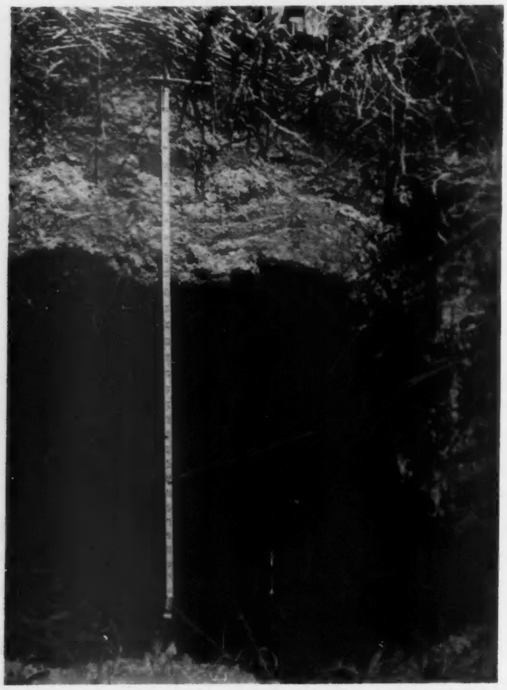

FIG. 19. Soil profile in *Calamagrostis canadensis-Angelica genuflexa*-Forbs community (Stand 24, see Fig. 18). Under the thick layer of straw an organic layer, 1 inch thick has formed since 1912 on the 10-inch layer of ash. Under the ash is a well developed silt loam to depth of about 27 inches. Working depth of roots at about 32 inches, maximum below 36 inches. June 24, 1949.

Because of the wide distribution of this community and because it gives a detailed description of the present condition of the ash layers deposited in 1912, the detailed description of the soil profile is given below.

The surface was covered with a loose 2-inch layer of straw and some moss upon a 0.5-inch layer of matted, moist plant debris.

0-1.0 inch. Dense fibrous material, many dead and live roots, small amount of mucky material and scattered ash grains, moist.

1-2.75 inches. Ash, pale brown, fine sand, single grain, very loose, appears leached, moist, roots and rhizomes numerous, roots finely branched, pH 5.6.

2.75-5.75 inches. Ash, brownish yellow with strong brown mottling, fine sand with some silt, much more compact than horizon above, picks out in loose irregular structures, moist, roots numerous but fewer than above, pH 5.4.

5.75-8 inches. Ash, very pale brown with irregular strong brown blotches which are somewhat more cohesive, picks out readily into usually single grains but also some loose irregular structures, moist, roots numerous, fewer than in horizon above, pH 5.6.

8-11.25 inches. Ash, light gray, fine sand with scattered white grains, some brown mottling and streaks along root channels, single grain, more compact than above, moist, roots numerous, pH 5.4.

11.25-15 inches. Dark reddish brown, largely humus, scattered argillite rocks 2 to 6 inches across in this horizon and below, moist, picks out in irregular structures which crumble readily, roots very numerous, pH 5.0.

15-20.5 inches. Reddish brown humus with some silt, heavier than layer above, upper part more compact than lower, picks out in irregular structures which crumble readily, roots numerous especially in upper half, pH 5.0.

20.5-26.75 inches. Silt with much humus and occasional argillite fragments, more compact than layer above, pin holes frequent, picks out in prisms which crumble rather crisply on pressure, moderately moist, roots numerous, pH 5.0.

26.75-36 inches. Light olive gray, clay with numerous argillite rock and gravel fragments, clay forming on rock surfaces, moist, roots frequent, decrease abruptly at 30 inches, working depth at 31.75 inches, very scarce at 35 inches, pH 5.2.

STAND 9 CALAMAGROSTIS CANADENSIS-EPILOBIUM ANGUSTIFOLIUM

The lower slopes of the hills bordering Anton Larsen Bay were covered with a dense stand of grassland and scattered clumps of shrubs, chiefly alders and elderberry. The alders formed almost impenetrable thickets along water courses. The grassland varied from almost pure stands of *Calamagrostis canadensis* to mixtures of this grass with tall forbs. Stand 9, an example of the latter was located on a slope of about 30°, facing southeast near the head of Anton Larsen Bay. It was studied on July 3, 1949.

Epilobium angustifolium appeared even more numerous in this stand than *Calamagrostis canadensis.* Somewhat less numerous were *Athyrium filix-femina, Trientalis europea arctica,* and *Sanguisorba sitchensis;* and moderately numerous were *Veratrum eschscholtzia,* very conspicuous because of its size, *Geranium erianthum, Deschampsia beringensis, Festuca rubra, Arenaria lateriflora,* and *Achillea borealis.* Less numerous to scarce were *Senecio triangularis, Solidago,* sp., *Heracleum lanatum,* and *Angelica lucida.*

Outstanding features of the soil profile were 1) the depth of the surface horizon, 1.5 inches, formed since 1912, 2) ash deposit between 1.5 and 11.75 inches, 3) the silt humus layer at 11.75-27.75 inches, 4) the numerous decomposing rock fragments in the lower part, 5) large number of roots to working depth at 30 inches, maximum 39 inches.

STAND 10 CALAMAGROSTIS CANADENSIS

This stand, located near the preceding on an east-facing slope of about 45°, was made up almost entirely of this one species, and scattered *Veratrum eschscholtzia.* It was studied on July 3, 1949. The grass was 3.5 inches high, but the heads were not out yet. A layer of dry straw, 2.5-3 inches thick, covered an inch-thick mat of plant debris, roots, and rhizomes on the surface.

The soil profile showed considerable resemblance to the one in the preceding stand. The organic layer at 0-1.75 inches was slightly thicker and contained more rhizomes; the ash layers were not so thick, extending down to 9.75 inches; the horizons rich in humus did not extend so deeply, terminating at 25.75 inches; and the working and maximum depths, 23.5 and 29 inches, were much more shallow. The layer of straw and the thick sod made invasion by other species difficult.

STAND 29 CALAMAGROSTIS CANADENSIS-CAREX MACROCHAETA-ANGELICA LUCIDA

This stand was located near the uppermost altitude for this community on Kodiak Island (Fig. 20). It was situated on a 30° to 40° slope, facing northwest, above the Ski Chalet, between the Naval Air Station and Anton Larsen Bay, at an elevation of about 1500 feet. On July 2, 1949, *Calamagrostis canadensis* was 10 to 18 inches high and had no flower stalks, and *Carex macrochaeta* was 6 to 8 inches high. These two were very abundant and dominant. *Angelica lucida,* 6 to 12 inches high, was moderately abundant. Other species were: *Epilobium angustifolium,* 12 to 15 inches high, *Alnus fruticosa* 2 to 3 feet tall, *Viola langsdorfii, Luzula multiflora, Geum calthifolium,* and species of *Hypnaceae.*

On spots where the gravel and rocks were within 3 to 4 inches or less of the surface dwarf heath shrubs were dominant, chiefly *Empetrum nigrum* and *Vaccinium uliginosum,* with scattered plants of *Artemisia arctica* and *Petasites hyperborea,* and some of the species listed above.

Outstanding features of the soil profile were 1) the fibrous organic layer at 0-1 inch, covered by 1 to 4 inches of plant debris, 2) most of the 1912 ash deposit had been blown or washed away, leaving a layer about 1.5 inches thick, 3) the thick humus layer at 2.5-22 inches, indicating that a well developed stand has existed here for a long time and was probably little disturbed by the ash fall, 4) an apparently earlier ash deposit at 22-28 inches, below which was gravelly clay, 5) numerous roots to the working depth at 29 inches, maximum about 38 inches.

FIG. 20. *Calamagrostis canadensis-Carex macrochaeta-Angelica lucida* community (Stand 29), at 1500 feet, Kodiak Island. Anton Larsen Bay in the distance. The ash was only 1.5 inches thick under the surface humus which was an inch thick. Numerous roots to depth of 29 inches in the humus-rich soil. July 2, 1949.

STAND 31 CALAMAGROSTIS CANADENSIS-CAREX MACROCHAETA-FORBS

The vegetation on the plateau-like top of Narrow Point, about 45 miles south of the Naval Air Station on Kodiak Island, resembled the *Calamagrostis canadensis*-Forbs community (Stand 16) on Isthmus Bay Point, but there were more hummocks of moss, the cover was less, and the number of species fewer. The elevation was about 200 feet, and it was exposed to the cold winds from the Pacific Ocean. The geological formation is different from most of this part of Kodiak Island, consisting of rather massive, fine-grained buff sandstone, of Miocene or Pliocene age, occurring on slate-graywacke beds (Capps, 1937).

The stand studied on June 19, 1949, was about 2 miles from the coast. The hummocks on the surface ranged from less than a foot to 2 feet wide, several yards long, and 3 to 12 inches high. The number of plants per unit of surface appeared to be fewer in the depressions than on the hummocks, and there were probably more grasses and fewer forbs in the depressions. The snow remains longer in the depressions, as indicated by the matted down vegetation.

The most common species were: A) numerous to very numerous; *Calamagrostis canadensis, Carex machrochaeta, Campanula rotundifolia, Galium boreale, Sanguisorba sitchensis, Angelica lucida, Epilobi-*

um angustifolium, Equisetum arvense, Achillea borealis, Solidago sp. (?), *Trientalis europea arctica,* and *Festuca* sp. (?); B) moderately numerous; *Lupinus nootkatensis, Viola langsdorfii,* and *Geranium erianthum;* C) few; *Hierochloa odorata, Veratrum eschscholtzia,* and *Luzula multiflora;* D) scarce; *Orchis aristata, Conioselinum benthami, Fritillaria camtchatkensis, Castilleja unalaschkensis* (?), *Parnassia palustris, Poa* sp., and *Heracleum lanatum.*

Important features of the soil profile were 1) the variation of the ash layer from 5 to 15.5 inches in thickness, due to the hummocky surface upon which it fell, 2) dark colored soil extended to depths of 29 to 33.5 inches, 3) roots numerous to the shallow working depth at 17 inches, 4) surface horizons indicated that soil development is proceeding rather rapidly, 5) surface was probably better drained in 1949 than prior to 1912, due to the ash.

STANDS 27A, 27B, 27C CALAMAGROSTIS CANADENSIS-FORBS

These stands were located on the site of the former agricultural experiment station near Buskin Lake on Kodiak Island. The station was officially closed in June, 1931; and there was no tillage after 1928-30 (E. C. Elting, 1951). Examination on July 5, 1949, revealed that the grassland was of three kinds on the south slope of less than 5°, A) not plowed, B) plowed and cultivated for a longer time than C) which may have been plowed only once.

Stand 27A. Not Plowed. The chief species were *Calamagrostis canadensis, Epilobium angustifolium, Equisetum arvense,* and the mosses *Pleurozium schreberi* and *Polytrichum* sp. Outstanding features of the soil profile were 1) the 2-inch layer of litter and moss on the surface with fibrous organic horizon at 0-1.25 inches, 2) moderately thick ash layer at 1.25-9.5 inches, 3) partly decayed vegetation at 9.5 inches, covered by the ash fall in 1912, 4) comparatively thin humus layer below the ash, underlaid by slate and argillite gravel, 5) roots numerous to working depth at 20 inches (cf. Kellogg & Nygard 1949, p. 65).

Stand 27C. Plowed and Cultivated for a Longer Time. This stand was near the preceding and had been under cultivation. The chief species were *Calamagrostis canadensis, Deschampsia beringensis,* and *Equisetum arvense.* The soil to a depth of 11 or 12 inches consisted of intermixed light gray to light brown ash and dark brown humus material. Below this plowed layer the profile was similar to that of the undisturbed soil. The aim in the deep plowing was evidently to mix the ash with some of the underlying material, but partly because of the thickness of the ash and the small amount of underlying material that was turned up the ash was changed very little. Only slight development has taken place since it was last tilled. The surface had a slight crust due to the growth of small moss plants. The uppermost 0.25 inch was paler in color than below.

Stand 27B. Plowed and Cultivated for a Short Time. This area had been plowed or cultivated less than 27C, and had probably been abandoned earlier. The chief species were *Calamagrostis canadensis, Deschampsia beringensis, Carex macloviana,* and *Lupinus nootkatensis.*

The plowed layer was 12 to 13 inches deep. As compared to the non-plowed profile, the sandy ash between 5.25 and 9.5 inches was brought upward, most of the 2-5.25-inch layer went downward but portions were scattered, and some of the gravel and clay from the 9.5-10.5-inch and the 10.5-19-inch horizons was also scattered. There was much more dark soil and less ash near the surface than in Stand 27C, and it was slightly harder to dig into.

Apparently the longer the cultivation was continued the more sandy the texture became, while the organic matter and clay decreased. The soil became looser and could be washed or blown away more easily. The plowing and cultivation of this land, with its layer of ash about 8 inches thick, had a detrimental effect on the development of the soil.

Species favored by plowing were *Lupinus nootkatensis, Deschampsia beringensis, Carex macloviana, C. mertensii, Rumex acetosella, Elymus mollis, Hordeum brachyantherum, Poa* spp., *Festuca rubra,* and several cultivated species including *Trifolium repens, T. pratense, Fragaria* sp., *Phleum pratense, Poa compressa,* and *Bromus* sp. Some species, present on the non-plowed area in 1949, had not yet appeared on the cultivated areas, such as *Castilleja unalaschkensis, Veratrum eschscholtzia, Polemonium acutiflorum, Galium boreale, Cicuta douglasii,* and *Angelica lucida.* Mosses were more abundant on the non-plowed land.

STAND 33 CALAMAGROSTIS CANADENSIS

This stand was situated on the uplands about 7 miles northwest of Homer at an elevation of about 900 feet (Fig. 21). The surface was very hummocky, due to ridges and mounds a foot or so high, covered with dense growth of *Calamagrostis canadensis.* Narrow depressions, serving also as drainage channels, separated the mounds and hummocks. On July 6, 1949, the following species were observed on the summit of the plateau and on the gentle upper slopes; *Calamagrostis canadensis,* about 90% of the cover, *Epilobium angustifolium* 8%, *Equisetum arvense* 2%, and scattered *Trientalis europea arctica, Sambucus racemosa pubens, Equisetum sylvaticum, Dryopteris austriaca, Streptopus amplexifolius, Lupinus nootkatensis, Geranium erianthum, Ribes laxiflorum,* and *Heracleum lanatum.* On lower slopes *Epilobium* and *Equisetum* were relatively more numerous. Grassland fires have been frequent in this region, retarding the growth of trees (Fig. 21), which occur as thickets of Sitka spruce and alder mostly.

Outstanding features of the soil profile were 1) the thick 3-10 inch layer of straw on the surface which retards the thawing of the soil, 2) the large amount of fibrous and mucky material to depth of 15 inches and silt loam below to 41 inches, 3) frozen ground between 12 and 20 inches on July 6, 1949, 4) two

FIG. 21. *Calamagrostis canadensis* community (Stand 33), with scattered Sitka spruce and clumps of alder, on the uplands about 7 miles northwest of Homer. Fire has been of frequent occurrence. The thick layer of straw retards thawing of the soil. July 6, 1949.

thin charred layers in the 0-1.5-inch horizon indicating former fires (Kellogg & Nygard 1949, p. 55, reported charcoal in the upper 6 to 10 inches of a soil profile in this region), 5) the large number of roots to 26 inches, working depth at 30 inches, maximum 38 inches, 6) hardness of the soil in the lowest horizon, 7) considerable soil development to 29.5 inches, 8) thick layer of straw and dense sod make plowing and cultivation more difficult and increase the fire hazard.

STAND 47 CALAMAGROSTIS CANADENSIS-EPILOBIUM ANGUSTIFOLIUM-RUBUS STRIGOSUS

This stand was situated on the west-facing slope (about 10°) of a hill about 1.5 miles west of Palmer, elevation about 275 feet, and was studied on July 19, 1949. The stand was typical of many grassland areas on hillsides in the Matanuska Valley, more or less surrounded by birch-white spruce forest. The plants were tall and dense, consisting mostly of *Calamagrostis canadensis* (locally called "redtop"), up to a height of about 6 feet. In this stand *Epilobium angustifolium,* 3 to 4 feet high, was very numerous, and *Rubus strigosus* moderately numerous. *Poa* sp. formed an understory at about 2 feet. There were 14 vascular species. This stand was similar to Stand 24 on the southeast-facing slope of Kalsin Bay, where *Rubus spectabilis* took the place of *R. strigosus,* and alder made up the thickets.

Judging by the character of the soil profile in this stand, and many similar areas in this region, as well as in the Homer region (Stand 33), this has been grassland for a long time. The charred fragments in the soil and the scattered burned logs and stumps indicated that fire has occurred frequently, which has favored the maintenance of grassland. The thick layer of plant debris has retarded the invasion of trees, and increased the fire hazard, especially during the dry months of May, June, and part of July. The thick layer of straw has also retarded the thawing of the ground in the spring.

Important features of the soil profile were 1) the large quantity and thickness of plant debris on the surface forming a layer a foot deep, 2) the loose fibrous and organic material and plant debris in the 1-10-inch horizon, 3) the dark layer of silt loam of good texture and structure at 10-15.5 inches, underlaid by silt to 24.5 inches, 4) frozen ground at 24 inches, 5) excellent root distribution and very numerous roots to 21 inches, working depth at about 23 inches, 6) charred wood in the 0-1-inch horizon, 7) decaying wood fragments to 24.5 inches, 8) reaction pH 5.2-5.6, 9) soil below 10 inches very favorable for tillage, portion above 10 inches needs further decomposition and incorporation with the deeper soil.

STAND 43 CALAMAGROSTIS CANADENSIS-EQUISETUM SYLVATICUM

This stand showed considerable similarity to the preceding and was representative of a large area of grassland on the west-facing lower slopes of the Chugach Mountains forming the eastern boundary of the Matanuska Valley. It was located at an elevation of about 600 feet, slope about 20°, on Lazy Mountain, and was studied on July 14, 1949. Besides the 2 listed above the chief species were *Epilobium angustifolium* and *Equisetum arvense.* As shown in Table 5 there were only 8 vascular species, the cover was excellent, 1532 hits.

Outstanding features of the soil profile (Fig. 22) were 1) the thick layer of loose straw, making a

FIG. 22. *Calamagrostis canadensis-Equisetum sylvaticum* community (Stand 43) on Lazy Mountain, east of Palmer. Soil is well developed to 35 inches, roots numerous to working depth of 35 inches, carbonized material to 20 inches. July 14, 1949.

pronounced fire hazard, 2) the large amount of organic matter in the upper horizons, 3) good soil development to 35 inches, 4) carbonized material to 20 inches, indicating former fires, 5) fragments of birch roots between 2 and 13 inches, 6) roots numerous to working depth at 35 inches, maximum 37 inches, 7) area has been in grassland with scattered trees for a long time.

STAND 49 CALAMAGROSTIS CANADENSIS-DRYOPTERIS DISJUNCTA-EPILOBIUM ANGUSTIFOLIUM

This stand was situated on a small flood plain at the mouth of the Little Susitna River Canyon on the south side of the Talkeetna Mountains, elevation about 1000 feet, north of Palmer. On June 13, 1949, the vegetation averaged about 3 feet high, ranging from 1.5 to 6 feet. Inflorescences of *Calamagrostis canadensis* were beginning to expand and those of *Epilobium angustifolium* were emerging. Ferns were common in a lower stratum. Other prominent species were *Mertensia paniculata, Rubus strigosus, Rosa acicularis,* and *Equisetum sylvaticum.* As shown in Table 5 the total number of vascular species was 23. The cover was rather low, 751 hits. The vegetation in this stand resembled that in the two preceding stands, but contained more species. The soil contained much more sand and gravel.

Outstanding features of the soil profile were 1) the 2-inch layer of plant debris on the surface and the high organic content of the 0-2-inch horizon, 2) silt loam horizon at 2-5.5 inches, 3) the alternation of sand and gravel layers and modified ash deposits to 41 inches where large rocks were found, 4) the conspicuous former surface horizon at 16.75 inches, 5) the large number of roots to the working depth at only 11.75 inches, and the rapid diminution of roots to the maximum at only 29 inches.

STAND 51 CALAMAGROSTIS CANADENSIS-DRYOPTERIS-ATHYRIUM-FORBS

This stand, situated on the south-facing slope, 5 to 10°, at an elevation of about 2400 feet, was typical of large areas in the Talkeetna Mountains, north of Palmer. It was studied on July 24, 1949. Tall forbs were conspicuous in the dense vegetation. The most prominent were *Heracleum lanatum,* blooming at 6 feet, *Veratrum eschscholtzia,* blooming at 5 feet, and the following at a height of 3 to 3.5 feet; Calamagrostis, *Geranium erianthum, Sanguisorba sitchensis, Aquilegia formosa, Epilobium angustifolium* (almost in bloom), *Aconitum delphinifolium.* The ferns, *Athyrium filix-femina, Dryopteris austriaca,* and *D. disjuncta,* made up a large part of the cover. There were 31 vascular species, 28 of which were hit.

Outstanding features of the soil profile were 1) the large quantity of plant debris on the surface, making a mat 4 to 5 inches thick, 2) dark colored silt loam, silt, and gravelly silt to 28.75 inches, 3) a gray podsolized layer at 2.75-4 inches, 4) the large number of boulders below 5.75 inches, 5) the very dark 5.75-10.75-inch horizon, possibly a former surface horizon upon which ash was deposited, 6) the extreme compactness of the gravel, with sand and rocks, below 28.75 inches, 7) roots numerous to working depth at 21 inches, few below that to maximum at only 26 inches, 8) profile indicates an old grass-forb community.

STAND 56 CALAMAGROSTIS CANADENSIS-FESTUCA ALTAICA-FORBS

This stand, studied on July 27, 1949, was situated at an elevation of about 3000 feet on the south slope (10-15°) of the Talkeetna Mountains north of Palmer. It showed much resemblance to the preceding stand and was representative of extensive areas between 2500 and 3000 feet. Granite rocks and boulders were scattered over the surface. In places shrubs, such as alders, willows, Spiraea, and Rubus formed thickets. This was one of the highest elevations at which *C. canadensis* was abundant and one of the dominants. The stand was very dense to a height of about 12 inches. The plant cover was excellent, index of 1786 hits. As in Stand 51, tall herbs were very conspicuous and made up most of the cover (Table 5). The most abundant forbs, constituting about 40% of the cover were *Valeriana sitchensis* with many flowers at 24 to 30 inches, *Sanguisorba sitchensis, Athyrium filix-femina, Geranium erianthum,* blooming at 20 inches, and *Dryopteris disjuncta.* Other conspicuous tall forbs were *Mertensia paniculata, Epilobium angustifolium, Castilleja unalaschkensis* with flowers at 12 to 16 inches, *Aconitum delphinifolium, Streptopus amplexifolius, Veratrum eschscholtzia, Senecio triangularis, Heracleum lanatum,* and *Aquilegia formosa.* The shrub *Spiraea beauverdiana* was scattered. Grasses made up only 20% of the cover. The more alpine conditions were indicated by the presence of heath species such as *Empetrum nigrum* and *Vaccinium caespitosum.* The leaves of *Calamagrostis canadensis* were 18 inches high, those of *Festuca altaica* 16 inches. Conditions were evidently more suitable for the latter because it had inflorescences at 20 to 26 inches while the former had none. There were 39 vascular species, 33 of which were hit.

Important features of the soil profile were 1) a one-inch layer of plant debris and moss on the surface, 2) the very dark silt loam to 14.5 inches and gravel and sand, with some silt and many rocks at 14.5-22 inches, 3) numerous roots, comparatively shallow in view of the good growth above ground, depth limited evidently by the compact soil below 20 inches, working depth about 17 inches, maximum 20 inches, 4) ample moisture, well drained, 5) stones scattered throughout and large boulders below 14 inches, 6) no effervescence, reaction pH 4.4-5.2, 7) an old grassland community indicated by the profile.

OTHER CALAMAGROSTIS CANADENSIS STANDS

Numerous other stands in which *Calamagrostis canadensis* was the chief dominant were examined in the summer of 1950, but were not analyzed by the

point-contact method. On the plain and in the hilly country north of Nome small areas occupied by *C. canadensis* grassland were found in places alternating with sedge-heath-lichen, willow, or scrub birch communities on ground which had been disturbed such as ridges along drainage ditches, roadsides, etc.; on hummocks and mounds in marshy land; and on slopes of stream valleys. Associated species were *Festuca altaica, Empetrum nigrum, Loiseleuria procumbens, Vaccinium uliginosum, Carex* spp., *Gentiana glauca, Petasites frigidus, Epilobium angustifolium, Angelica lucida, Spiraea beauverdiana, Poa arctica, Polemonium acutiflorum Rubus arcticus,* mosses, and lichens.

Examination of a soil profile in a stand where 1949 stalks reached a height of 2.5 feet, on a slope of less than 5°, near Nome on July 8, 1950, showed a 2-inch layer of loose straw, partly decomposed in the lower part. The 0-1-inch horizon was mostly decomposed plant debris, wet, very numerous roots, pH 5.2. Between 1 and 13 inches the fine fibrous peat was dark dusky red, saturated, scattered pockets of dark brown silt loam rich in organic material, fine roots very numerous, frozen at 13 inches, pH 5.2.

On the upland about 3 to 4 miles west of Kotzebue, where most of the vegetation consisted of the cotton grass-sedge-dwarf shrub complex and sedge-sphagnum, small stands of *Calamagrostis canadensis* with *Epilobium angustifolium* as the chief associate were found. Larger stands occurred on southeast-facing slopes, with considerable intermingling of sedges, scattered willows, dwarf shrubs, and 2- to 4-inch tall lichens in the open spaces.

In the vicinity of the McKinley Park Hotel, at the east end of McKinley Park, *C. canadensis* is one of the early invaders following disturbance of the original vegetation by burning, bulldozing, etc. Other early invaders were *Agrostis scabra, Epilobium angustifolium, Hordeum jubatum, Parnassia palustris, Equisetum arvense, E. sylvaticum, Achillea borealis, Castilleja pallida, Poa* sp., *Luzula multiflora, Artemisia tilesii,* mosses, and *Mertensia paniculata.* On extensive areas of the lower mountain slopes which had been burned over in about 1926 *C. canadensis* was the chief dominant. Associated species were *Polygonum alaskanum, Epilobium angustifolium, Spiraea beauverdiana,* Polytrichum, and scattered *Alnus fruticosa* and *Juniperus communis montana.*

Medium Tall Grass-Forb Communities with Festuca altaica as the Chief Dominant

Six stands, ranging in location from Kodiak Island to the Talkeetna Mountains and Healy, studied in detail, are classified in this group. They show similarity in that the *Festuca altaica* is the chief dominant in each and the presence of common species in at least several, such as *Calamagrostis canadensis, Epilobium angustifolium, Achillea borealis, Mertensia paniculata, Aconitum delphinifolium, Luzula parviflora,* and *Solidago multiradiata.* Some of these communities at the lower elevations were very similar to those in the preceding series in which *C. canadensis* was the chief dominant; and some at higher elevations are transitional to the heath or Dryas-sedge types of communities. They are similar to Nordhagen's (1943) associations in Norway in the tall herb mountain meadows order (*Aconitetalia*).

Stand 30 Festuca altaica

This stand was situated in a broad valley at an elevation of about 650 feet in the mountains on the divide between the Naval Air Station and Anton Larsen Bay, Kodiak Island. The slope was less than 5°, the surface was slightly hummocky. On July 21, 1949, the vegetation appeared dense because of the presence of the herbage of previous years, but the cover was low, only 621 hits. *Festuca altaica,* 6 to 10 inches tall, made up about one-third of the cover and mosses over one-third (Table 6). Other prominent species were *Calamagrostis canadensis,* 8-12 inches tall, *Angelica lucida,* 6-8 inches, *Epilobium angustifolium,* 6-10 inches, and *Achillea borealis.* The total number of species was 16, only 7 of which were hit. This stand resembled Stands 4 and 32 in the lowlands.

Outstanding features of the soil profile were 1) ash layer 7.25 inches thick beneath plant debris and moss, 1 to 3 inches deep, 2) organic layer at 7.25-17 inches indicated that a well developed grassland, probably similar to the present one, existed here prior to 1912, 3) clay, rich in organic matter at 17-21.5 inches, gravel and rocks below, 4) roots numerous to 27 inches, the working depth, 5) soil apparently forming from slate and argillite rocks, especially below 21.5 inches, 6) reaction pH 4.6-5.6.

Stand 48 Festuca altaica-Forbs

This stand, studied on July 10, 1949, was at an elevation of about 1900 feet on the first bench above the river in the Little Susitna Valley in the Talkeetna Mountains, north of Palmer. The southeast-facing slope was less than 5°. Snowslides from the nearby steep mountain slopes pass onto this site occasionally, as shown by scattered pieces of alder stems. Many alders were decumbent in the adjoining draws. The abundance of many species of tall forbs in mixture with tall grasses (Table 6) was a characteristic feature of this stand (Fig. 23). *Festuca altaica* made up only about 17% of the total cover, and *Calamagrostis canadensis* constituted about half as much cover. The other chief species were *Dryopteris disjuncta, Cornus canadensis intermedia, Vaccinium caespitosum, Geranium erianthum, Sanguisorba sitchensis, Fritillaria camtchatcensis,* and *Epilobium angustifolium.* Other characteristic species were *Anconitum delphinifolium, Mertensia paniculata,* and *Veratrum eschscholtzia.* The total number of species was 21, 27 of which were hit.

Outstanding features of the soil profile were 1) the deep brown soil to 19.5 inches, 2) three layers of volcanic ash distinguished, 3) the powdery, leached 2-4-inch horizon, 4) an old stand as shown by the deep soil development, the topography, and the fibrous 0-2-inch

TABLE 6. Medium Tall grass-Forb Communities with *Festuca altaica* as the Chief Dominant.

Species	Stand 30 Kodiak		Stand 48 Talk. Mts.		Stand 55 Talk. Mts.		Stand 79 Healy		Stand 83 McK. Park		Stand 80 McK. Park	
	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %
Festuca altaica	230	100	195	95	503	80	649	100	706	100	183	90
Festuca rubra	4	5										
Calamagrostis canadensis	41	50	99	80	15	15	28	25				
Calamagrostis sp.	..	..	..	..	..	..	..	..	..	..	3	5
Deschampsia atropurpurea	..	..	8	10	24	30						
Phleum alpinum	..	..	x	..	25	10						
Poa arctica	..	..	..	..	..	..	..	..	37	35		
Poa paucispicula	..	..	..	..	..	..	..	..	..	..	2	10
Poa sp.	..	..	x	..	23	10	4	15				
Trisetum spicatum	..	..	..	..	2	10	..	..	1	5		
Danthonia intermedia	..	..	..	..	6	5						
Elymus innovatus	..	..	..	..	..	..	60	30				
Arctagrostis latifolia	..	..	..	..	..	..	..	..	2	10	1	5
Hierochloe alpina	..	..	..	..	..	..	..	..	..	..	2	5
Poaceae	..	..	..	..	2	5						
Carex spectabilis	..	..	41	30								
Carex brunnescens	..	..	1	5								
Carex anthoxanthea	..	..	..	..	24	30						
Carex macrochaeta	..	..	..	..	6	10						
Carex obtusata	..	..	..	..	..	..	17	20				
Carex praticola	..	..	..	..	..	..	1	5				
Carex montanensis	..	..	..	..	..	..	..	..	417	95		
Carex bigelowii	..	..	..	..	..	..	..	..	40	10		
Carex bipartita	..	..	..	..	..	..	..	..	x			
Carex podocarpus	..	..	..	..	..	..	..	..	..	..	46	70
Carex sp.	..	..	..	..	25	25						
Luzula parviflora	..	..	13	25	3	5	..	..	3	5	8	10
Luzula rufescens	..	..	..	..	..	..	7	20				
Luzula multiflora	..	..	..	..	..	..	..	..	5	15		
Epilobium angustifolium	10	50	44	65	9	20	23	45				
Epilobium latifolium	..	..	..	..	3	5	..	..	..	..	x	
Epilobium alpinum	..	..	..	..	11	20						
Mertensia paniculata	..	..	17	10	..	..	25	35	20	50	3	5
Achillea borealis	23	20	17	40	34	70						
Solidago multiradiata	4	5	..	..	..	..	..	..	31	30	x	
Angelica lucida	39	35										
Sanguisorba sitchensis	..	..	52	70	46	65						
Geranium erianthum	..	..	62	75	25	35						
Fritillaria camtchatcensis	x	..	47	65								
Artemisia arctica	..	..	..	..	18	35	..	..	56	65	12	40
Artemisia tilesii	..	..	..	..	..	..	..	..	..	..	3	5
Viola adunca	x	..	11	25	17	40						
Viola sp.	..	..	..	..	2	5						
Castilleja unalaschkensis	..	..	25	40								
Aconitum delphinifolium	..	..	6	20	4	10	..	..	9	30	7	15
Veratrum eschscholtzia	x	..	1	5								
Lupinus nootkatensis	x	..	8	5	x							
Lupinus podophyllus	..	..	..	..	..	..	..	..	8	10		
Arenaria lateriflora	..	..	7	25	1	5	10	30	1	5		
Equisetum arvense	..	..	..	..	..	..	..	..	..	..	8	20
Equisetum scirpoides	..	..	..	..	..	..	2	5	..	..	5	15
Equisetum pratense	..	..	..	..	..	..	x					
Equisetum alaskanum	..	..	..	..	..	..	..	..	1	5		
Dryopteris disjuncta	..	..	94	80								
Dryopteris oreopteris	..	..	12	10								
Botrychium boreale	..	..	..	..	x							
Botrychium lunaria	..	..	..	..	..	..	..	..	..	..	x	
Lycopodium clavatum	x											
Lycopodium alpinum	..	..	..	..	42	45						
Cornus canadensis intermedia	..	..	81	80								
Trientalis europaea arctica	..	..	17	45	17	35						
Senecio triangularis	..	..	7	10								
Senecio lugens	..	..	..	..	..	..	..	..	17	30		
Sibbaldia procumbens	..	..	..	..	19	25						
Antennaria monocephala	..	..	..	..	7	5	..	..	4	10	4	10
Antennaria isolepis	..	..	..	..	x							
Ranunculus occidentalis	..	..	..	..	5	15						

TABLE 6—Continued

Species	Stand 30 Kodiak		Stand 48 Talk. Mts.		Stand 55 Talk. Mts.		Stand 79 Healy		Stand 83 McK. Park		Stand 80 McK. Park	
	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %
Veronica wormskjoldii	..	..	..	..	4	20						
Campanula lasiocarpa	..	..	..	..	2	5	..	..	..	..	2	10
Erigeron peregrinus	..	..	..	..	2	5						
Polygonum viviparum	..	..	..	..	1	5	..	..	..	..	2	5
Polygonum bistorta plumosum	..	..	..	..	..	..	..	..	24	70	2	10
Polygonum alaskanum	..	..	..	..	..	..	x					
Saxifraga bronchialis funstonii	..	..	..	..	1	5						
Saxifraga reflexa	..	..	..	..	..	..	2	5				
Saxifraga tricuspidata	..	..	..	..	..	..	x					
Saxifraga hieracifolia	..	..	..	..	..	..	..	..	3	10	x	
Saxifraga punctata	..	..	..	..	..	..	..	..	..	..	x	
Pedicularis verticillata	..	..	..	..	1	5	..	..	x			
Pedicularis capitata	..	..	..	..	1	5	..	..	..	..	3	10
Claytonia sarmentosa	..	..	..	..	x							
Claytonia sp	..	..	..	..	..	..	..	..	2	5	x	
Anemone parviflora	..	..	..	..	..	..	..	..	6	15	3	5
Anemone narcissiflora	..	..	..	..	..	..	5	5	20	45		
Anemone richardsonii	..	..	..	..	..	..	..	..	1	5		
Galium boreale	..	..	..	..	..	..	19	25				
Gentiana propinqua	..	..	..	..	..	..	9	30				
Linnaea borealis	..	..	..	..	..	..	14	25	..	..	8	5
Stellaria longipes	..	..	..	..	..	..	6	20	34	40		
Stellaria laeta	..	..	..	..	..	..	..	..	..	..	4	20
Polemonium acutiflorum	..	..	..	..	..	..	..	..	33	40		
Cerastium beringianum	..	..	..	..	..	..	..	..	18	50		
Thalictrum alpinum	..	..	..	..	..	..	..	..	17	40		
Valeriana capitata	..	..	..	..	..	..	..	..	12	35		
Petasites frigidus	..	..	..	..	..	..	..	..	4	5		
Myosotis alpestris	..	..	..	..	..	..	..	..	4	10	x	
Dodecatheon frigidum	..	..	..	..	..	..	..	..	2	10		
Astragalus umbellatus	..	..	..	..	..	..	..	..	x			
Sedum roseum	..	..	..	..	..	..	..	..	x	..	7	5
Saussurea angustifolia	..	..	..	..	..	..	..	..	..	..	2	5
Boykinia richardsonii	..	..	..	..	..	..	..	..	..	..	x	
Parnassia kotzebuei	..	..	..	..	..	..	..	..	..	..	x	
Seedling	..	..	3	5								
Salix barclayi	x											
Salix glauca	x	..	..	..	..	..	4	5				
Salix sitchensis	x											
Salix reticulata	..	..	..	..	53	55	..	..	..	..	3	5
Salix polaris selynensis	..	..	..	..	9	25						
Salix sp	..	..	..	..	..	..	..	..	x			
Populus tacamahacca	..	..	..	..	..	..	x					
Populus tremuloides	..	..	..	..	..	..	x					
Picea glauca	..	..	..	..	..	..	x					
Betula nana exilis	..	..	..	..	..	..	x	..	x	..	28	15
Spiraea beauverdiana	x											
Rubus stellatus	..	..	9	40	24	55						
Rubus alaskensis	..	..	2	5								
Vaccinium caespitosum	..	..	102	60	27	45						
Vaccinium uliginosum	..	..	..	..	7	5	62	20	..	..	107	70
Vaccinium vitisidea	..	..	..	..	..	..	147	65	..	..	163	75
Rosa acicularis	..	..	..	..	..	..	5	5				
Empetrum nigrum	..	..	..	..	9	15	..	..	..	..	155	55
Luetkia pectinata	..	..	..	..	30	45						
Arctostaphylos uva-ursi	..	..	..	..	..	..	x					
Dryas octopetala	..	..	..	..	..	..	..	..	..	..	130	70
Cassiope tetragona	..	..	..	..	..	..	..	..	..	..	9	5
Pyrola grandiflora	..	..	..	..	..	..	..	..	..	..	2	5
Ledum decumbens	..	..	..	..	..	..	..	..	..	..	x	
Hypnaceae spp	157	100	136	75	200	100	x	..	x	..	x	
Polytrichum sp	113	80	35	20								
Lichens	..	..	..	..	..	..	x	..	..	..	x	
No hits	..	..	..	..	..	..	8	..	..	..	2	
Total number of hits	621	..	1151	..	1289	..	1099	..	1538	..	917	

FIG. 23. A well developed *Festuca altaica* community (Stand 48) in the Medium Tall Grass-Forb Community group. Prominent forbs are *Epilobium angustifolium*, *Sanguisorba sitchensis*, *Geranium erianthum*, *Cornus canadensis intermedia*, and *Dryopteris disjuncta*. The dark brown, well developed soil to depth of 19.5 inches indicates an old grassland. Talkeetna Mountains, north of Palmer, 1900 feet elevation, July 10, 1949.

layer, 5) roots dense to 10.5 inches, shallow working depth at 17 inches, maximum at 24 inches, 6) internal drainage good, 7) some horizons differentiated more by the "feel" and picking than by color, 8) lupine nodules at 12.5 inches.

Detailed description of the soil profile:

The surface was covered with a loose layer about an inch thick of leaves and stems, below which was a fairly compact layer of partly decayed plant debris and moss.

0-2 inches. Dry, fibrous, mostly organic matter partly decayed, many roots and rhizomes, pockets of brown silt.

2-4 inches. Brown, dries quickly, turning gray, very loose, silt loam, appears partly leached, moist, single grain, very many roots.

4-10.5 inches. Reddish brown, yellow brown mottling, silt loam, scattered granite particles, moist, many roots and rhizomes.

10.5-19.5 inches. Strong brown to dark brown, fine sand with coarse sand and gravel interspersed, irregular platy structure; a 1-inch lens in the middle consisting of brown sand, gritty, compact, with pin holes, platy, crumbles into single grains some of which are white, apparently volcanic ash; moist, roots frequent to working depth 17 inches.

19.5-29.5 inches. Yellowish brown, loose sand, coarse, many granite pebbles and rocks often crumbling on touching; at 20.5-21.5 inches gray ash, moist; roots scarce to maximum depth at 24 inches, except near a large rock where it was 30.5 inches.

29.5-31 inches. Volcanic ash, light brown gray, scattered white grains, pin holes present, breaks into rather coarse platy structures, gritty, moist, dries into fine, light gray powder.

31-36 inches. Yellowish brown, clay, sand and gravel interspersed, becoming sandier with depth, moist, sticky.

36-38.5 inches. Sand and gravel, becoming rocky with depth.

STAND 55 FESTUCA ALTAICA-FORBS

This stand was situated at 4500 feet, near Independence Mine, in the Talkeetna Mountains, north of Palmer. It was between the rocks where some soil had accumulated on a steep south slope, 30-40°. The cover was moderate, 1289 hits, and on July 27, 1949, consisted of 38% *Festuca altaica* in bunches 2 to 4 inches in diameter, 6 to 10 inches high, with only a few inflorescences. Other important species (Table 6) were *Sanguisorba sitchensis*, *Lycopodium alpinum*, *Salix reticulata*, *Luetkia pectinata*, *Achillea borealis*, and *Hypnaceae* spp. The total number of vascular species was 46, an interesting assemblage of plants from alpine nad lower zones.

Important features of the soil profile were 1) well developed dark soil (silt loam to silt) with scattered rocks to depth of 26.5 inches, indicating an old stand, 2) sandy loam between rocks at 26.5-31.5 inches, 3) abundance of roots to 31 inches, 4) reaction pH 5.2-6.2, 5) layer of litter was thin.

STAND 79 FESTUCA ALTAICA

This stand was located on a steep, 30-40°, east-facing slope, on the first bench above the Nenana River, about one-fourth mile northwest of the Healy railroad station. The elevation was about 1350 feet. It was studied on August 20, 1949. This was a small stand with willows, aspens, Alaska birches, and a few white spruce surrounding it and invading in places. Similar stands were scattered on this slope. The cover was moderate, 1099 hits. Much of this slope was at one time probably covered with this grassland following destruction of the trees by fire, and now the trees have taken over again most of the area. This slope was much moister than that on which Stand 77, *Elymus innovatus-Poa glauca* community, was located across the river on a south-facing slope. The total number of vascular species was 29, of which 21 were hit. The bunches of *Festuca altaica*, leaves 20-24 inches high, inflorescences up to 36 inches, made up 59% of the cover. *Calamagrostis canadensis* stalks were 18 to 22 inches high; *Epilobium angustifolium* 10 to 20 inches, *Mertensia paniculata* 12 to 18 inches, *Vaccinium uliginosum* 6 to 8 inches (Table 6).

Important features of the soil profile were 1) mosses and lichens formed a crust between grass tufts, 2) well developed silt-loam horizons to 3.5 inches, 3) gravel and sand with scattered stones at 3.5-38 inches, 4) roots very numerous to 21.5 inches, working depth at 22.5 inches, maximum 34 inches, 5) acid reaction, pH 4.6 to 6.6, acidity most pronounced in the 3.5-9.5-inch horizon.

STAND 83 FESTUCA ALTAICA-CAREX MONTANENSIS-FORBS

This stand was situated on the lower part of a south-facing slope, less than 5°, in outwash material from hills to the north, at an elevation of about 3600 feet, near Polychrome Pass, in Mt. McKinley National Park (Fig. 24). This type of community was wide-spread between the open stands of willows, 4 to 8 feet tall, and *Betula glandulosa*, 3 to 5 feet tall. It was studied on August 23, 1949. The chief species were *Festuca altaica* and *Carex montanensis*, making up about 46% and 27% respectively of the dense cover, 1538 hits. The basal diameter of the *Festuca* tufts was about 5 inches, leaves were 12 to 15 inches high, and the inflorescences 20 to 24 inches. Other prominent species were *Aconitum delphinifolium* blooming at 10 to 15 inches; *Mertensia paniculata*, last flowers at about 18 inches, *Artemisia arctica*, *Polemonium acutiflorum*, and *Solidago multiradiata*. Larger willows occurred in more gravelly soil at the margins of the stand. A total of 37 vascular species were found, of which 31 were hit, as shown in Table 6.

FIG. 24. *Festuca altaica-Carex montanensis*-Forbs community (Stand 83), willows and *Betula glandulosa* at left. Near Polychrome Pass, Mt. McKinley National Park, August 23, 1949.

FIG. 25. Soil profile in *Festuca altaica-Carex montanensis*-Forbs community (Stand 83, see Fig. 24) in Mt. McKinley National Park. Organic silt loam to 4.5 inches, yellowish brown silt at 4.5-8.5 inches, on top of a dark gray to brown silt layer (probably an old surface horizon), with pebbles and cobbles below. Frozen ground at 34 inches, roots numerous to 14 inches, shallow working depth at 18 inches. August 23, 1949.

Important features of the soil profile were 1) beneath a 1-inch layer of litter was an organic silt horizon, 2) well developed silt loam in the 1.5-4.5-inch horizon (Fig. 25), 3) the silt layer at 4.5-8.5 inches was probably washed in from higher land to the north, 4) the mottled silt horizon at 8.5-14 inches may have been formed while this area was a marsh, 5) below 14 inches silt, with much gravel and rock, 6) soil moisture increased with depth to saturation at about 26.5 inches, 7) frozen ground at 34 inches, 8) roots numerous to 14 inches, working depth at only 18 inches, some roots to the frozen ground, 9) acid reaction, pH 4.6-5.8.

STAND 80 FESTUCA ALTAICA-VACCINIUM VITISIDEA-V. ULIGINOSUM-EMPETRUM NIGRUM-DRYAS OCTOPETALA

The area occupied by this stand was a rocky, fairly homogeneous, south-facing slope of about 20 to 25°, at the high elevation of about 4000 feet, near Sable Pass, Mt. McKinley National Park. The ground between the rocks was usually gravelly. On August 21, 1949, the vegetation was mostly in tufts with lichens and mosses forming a complete cover when the tufts were close together, but much ground was exposed when the tufts were somewhat scattered. The tufts of *Festuca altaica*, with leaves 10 to 12 inches high, characterized the appearance of the stand, this species providing most of the cover. As shown in Table 6 the most important species were *Vaccinium vitisidea*, *V. uliginosum* 4 to 5 inches high, *Empetrum nigrum*, and *Dryas octopetala*. These 5 species made up the rather low total cover, 917 hits.

Important features of the soil profile were 1) abundance of roots, chiefly Festuca to working depth at 24 inches, maximum 32 inches, 2) gravel and stones, intermixed with silt loam, on the surface or close to the surface, 3) deep penetration of dark color, to 35 inches, 4) the dark gray brown horizon at 1.25-2.25 inches appeared leached, 5) pH 5.2-5.6.

OTHER FESTUCA ALTAICA STANDS

Small communities, often among willows or scrub birch, in which Festuca was the chief dominant were seen in the summer of 1950 on south-facing slopes of draws and creek valleys on the plain near Nome

and in the hilly country northeast of Nome, and very small patches on east-facing slopes along the Nome River 10 miles northeast of Nome. These communities show resemblance to Nordhagen's (1943) alpine fescue-grass-heath association (*Festucetum ovinae alpicolum*) in the Dry grass-Heath on Lime Poor Rock Order. They are considered excellent for grazing in Norway. Associated species in the stands in the Nome region were *Calamagrostis canadensis, Arctagrostis latifolia, Epilobium angustifolium, Taraxacum* sp., *Anemone narcissiflora, Viola adunca, Antennaria monocephala, Luzula* sp., *Lycopodium alpinum, Carex* spp., *Angelica lucida, Sedum roseum, Claytonia sarmentosa,* mats of *Empetrum nigrum* and *Loiseleuria procumbens* in open spots, *Pedicularis capitata, Vaccinium uliginosum, Salix reticulata, Artemisia arctica, Petasites frigidus;* scattered mosses especially *Polytrichum* sp., and lichens, especially *Cladonia alpestris, C. rangiferina, Cetraria islandica, Stereocaulon tomentosum,* and *Peltigera rufescens.*

A soil profile was examined in a stand on a steep, south-facing bank of Dry Creek near Nome on July 8, 1950, where the herbage was 2 feet high and the *Festuca* clumps 4 to 6 inches in diameter. On the surface was a layer 1 inch thick of dead leaves and moss. The 0-1-inch horizon consisted of decaying vegetation with numerous roots, pH 5.2; 1-9 inches, dark brown silt loam, excellent soil, moist, well drained, roots numerous, pH 5.2, 9-15 inches, brown silt loam with small rocks and gravel, roots frequent, pH 5.2.

On mostly south-facing slopes of ridges and mountains, and in open areas between willows, aspens, birches and spruces in the eastern end of Mt. McKinley Park, *Festuca altaica* communities are common. As observed on July 21-23, 1950, the commonest associates were *Empetrum nigrum, Vaccinium vitisidæa. Gentiana propinqua, Epilobium angustifolium, Solidago multiradiata, Rosa acicularis, Cornus canadensis, Linnaea borealis, Artemisia arctica, Saxifraga tricuspidata,* mosses, and lichens. Among the less numerous were *Aconitum delphinifolium, Viburnum edule, Poa glauca, Elymus innovatus, Alnus fruticosa, Populus tremuloides, Pedicularis sudetica, Anemone narcissiflora, Calamagrostis canadensis, Ledum groenlandicum, Zygadenus elegans, Mertensia paniculata, Lupinus nootkatensis, Aster sibiricus,* and *Equisetum scirpoides.*

Agropyron Trachycaulum Communities

Only 2 stands in this community were studied, both of them situated on steep, glaciated slopes west and southwest of Palmer. Both stands were characterized by 1) the thin stand in which most of the cover consisted of *Agropyron trachycaulum,* 2) species in common including *Epilobium angustifolium, Taraxacum* sp., *Achillea borealis, Poa* sp., *Rubus strigosus, Erigeron acris, E. asterioides,* and *Senecio pauciflorus* (see Table 7), 3) well developed and deep root systems, 4) soil fairly well developed to at least 1.5 feet. These stands resemble Nordhagen's tall herb mountain meadow communities (*Aconitetalia*) in Norway.

Stand 37. This stand studied on July 20, 1949, was on the upper part of a steep south-facing slope, about 30°, about 1.5 miles west of Palmer, at an elevation of about 275 feet. The lower parts and the west part of this hill were covered largely with the *Calamagrostis canadensis-Epilobium angustifolium-Rubus strigosus* community (Stand 47). Trees, including *Betula resinifera, Salix bebbiana,* and *Populus tremuloides,* and shrubs, *Rubus strigosus, Sambuccus racemosa pubens,* were scattered on the edges, and were abundant on the east- and north-facing slopes. The moderately dense cover, 1120 hits, consisted chiefly of *Agropyron trachycaulum* (68%). leaves 12-15 inches high and inflorescences up to 2 feet, *Epilobium angustifolium* blooming at 18 to 30 inches made up 11% of the cover, and *Rubus strigosus,* 10-18 inches high, 9% (Table 7). The total number of vascular species was 23, of which 14 were hit.

Outstanding features of the soil profile were 1) very numerous roots to 32.75 inches, deep working depth at 44.5 inches and maximum at 60 inches, 2) numerous horizons, silt to 44.5 inches, below which was rock and gravel with little silt and sand to 61 inches, 3) the well developed silt soil, especially in the upper 10.75 inches, indicating an old grassland, 4) charred wood, especially at 19-20 inches and as deep as 35 inches, 5) pH 6.8 to 8.0, 6) a 2-6-inch layer of straw on the surface.

Stand 38. This stand, studied on July 9, 1949, was located at elevation of about 100 feet, on a 30° south-facing slope of an esker on the border of the Matanuska River flood plain, about 1 mile east of Matanuska Junction. The cover was moderately dense, 1221 points, made up of about 48% *Agropyron trachycaulum.* Other conspicuous species were *Epilobium angustfolium* and *Taraxacum* sp. The total number of vascular species was 17, only 9 of which were hit. The top of the esker and the north-facing slope were covered with woods, made up chiefly of *Betula resinifera, Populus tremuloides,* and a few small, scattered *Picea glauca.*

Important features of the soil profile were 1) silt loam horizons to 19 inches, with scattered rocks below 15 inches, gravel and sand with scattered rocks and a little silt at 19-49 inches, 2) horizons not clearly differentiated, 3) good distribution of roots to 34 inches. even in the sand between rocks in lower part, fairly deep working and maximum depths at 38 and 47 inches, 4) charred wood as deep as 10 inches indicating old burns, 5) excellent surface and internal drainage, a loose soil, easy to dig, 6) surface well protected by plants and a thin layer of straw and moss, 7) an old grassland, shown by the deep development of the soil.

Miscellaneous Upland Grassland Communities

Six stands are grouped under this heading. The first 5 were situated on steep, south-facing hillsides

TABLE 7

Species	*Agropyron trachycaulum* Communities				Miscellaneous Upland Communities											
	Stand 37 Palmer		Stand 38 Palmer		Stand 61 Up. Mat. Val.		Stand 62 Up. Mat. Val.		Stand 63 Up. Mat. Val.		Stand 65 Tan. Val.		Stand 77 Healy		Stand 64 Donnelly	
	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %
Agropyron trachycaulum	753	100	770	100												
Poa sp.	46	40	17	20												
Agrostis sp.	5	10														
Elymus macounii			x													
Epilobium angustifolium	125	85	85	70											16	20
Achillea borealis	5	5	39	40									9	15		
Erigeron acris asterioides	x		6	5												
Taraxacum sp.	30	40	76	70												
Senecio pauciflorus	8	15	x													
Arenaria lateriflora	1	5	x										1	5	x	
Solidago multiradiata	12	15													x	
Equisetum pratense	7	15											2	5		
Castilleja pallida	5	10														
Aster sibiricus	1	5											10	20		
Antennaria nitida			27	5												
Antennaria pallida	x															
Parnassia palustris	x															
Geum macrophyllum	x															
Erigeron acris	23	55	6	5												
Erigeron acris elatus	x															
Oxytropis deflexa			11	10												
Mertensia paniculata	x															
Potentilla virgulata			x													
Lathyrus palustris			x													
Rhinanthus sp.			x													
Botrychium lunaria	x															
Rubus strigosus	99	65	6	15												
Populus tremuloides	x		x													
Betula resinifera	x															
Salix bebbiana	x															
Rosa acicularis			x													
Calamagrostis purpurescens					458	100	24	10	115	45	x		10	20	x	
Bromus pumpellianus					10	5	55	65	79	55						
Poa glauca					x		5	10	185	85	91	30	143	85		
Poa pratensis															11	15
Poa alpina															9	15
Agropyron spicatum											739	80				
Agropyron latiglume															137	85
Festuca rubra															676	100
Agrostis sp.															15	25
Elymus innovatus													514	100	7	5
Carex supina													41	25	146	90
Carex sp.											16	30				
Luzula multiflora															x	
Artemisia frigida					149	55	110	75	162	95	193	80				
Artemisia dracunculoides					8	10	37	25	16	20						
Potentilla pennsylvanica					23	20	13	35	13	30	7	10	21	55		
Potentilla chamissonis					12	10										
Potentilla arguta					x											
Potentilla nivea							x		8	15			1	5		
Antennaria oxyphylla					17	25					30	10				
Antennaria sp.									x							
Arabis holboellii					1	5					4	5				
Arabis divaricarpa							x									
Lychnis dawsonii							4	10								
Galium boreale					x		3	10	x		6	5	32	40		
Draba aurea							2	5					2	5		
Draba lanceolata							x		3	15						
Draba glabella															x	
Anemone multifida									3	5						
Anemone patens multifida											61	35	103	40		
Erigeron sp.											29	20				
Plantago canescens													44	45		
Plantago septata					x											

TABLE 7—Continued

Species	*Agropyron trachycaulum* Communities				Miscellaneous Upland Communities											
	Stand 37 Palmer		Stand 38 Palmer		Stand 61 Up. Mat. Val.		Stand 62 Up. Mat. Val.		Stand 63 Up. Mat. Val.		Stand 65 Tan. Val.		Stand 77 Healy		Stand 64 Donnelly	
	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %
Gentiana propinqua													8	20	x	
Saxifraga tricuspidata					x								15	5		
Saxifraga reflexa													1	5	x	
Equisetum arvense													4	5		
Stellaria longipes															51	65
Arenaria laricifolia															27	30
Oxytropis gracilis															24	30
Oxytropis viscidula							x									
Zygadenus elegans															15	20
Bupleuron americanum															9	30
Linum lewisii															4	5
Erysimum inconspicuum					x											
Polemonium pulcherrimum							x									
Androsace septentrionalis							x									
Smilacina stellata									x							
Selaginella sibirica											x					
Senecio coterminus															x	
Cerastium beringianum															x	
Astragalus alpinus															x	
Pedicularis verticillata															x	
Rosa acicularis					6	15	26	35	41	40	33	15	55	55		
Amelanchier alnifolia					x						3	5	2	5		
Juniperus horizontalis					x											
Rubus strigosus													2	5		
Moss			184	95							x		x		194	100
Cladonia sp.					65	75	105	80	54	50						
Lichens											x		x		x	
No hits	4				28		43		26		7		4			
Total number of hits	1120		1221		749		384		679		1212		1020		1341	

and mountain slopes; the sixth, quite distinct in its plant composition from the other 5, was in a mountain valley. The first 5 show similarity to one another by the presence of *Calamagrostis purpurescens, Poa glauca, Potentilla pennsylvanica, Rosa acicularis,* and *Galium boreale* in all of them; *Artemisia frigida* in 4; and *Bromus pumpellianus, Artemisia dracunculoides,* and *Amelanchier alnifolia* in 3. The first 5 stands appear to be northwestward outliers of grassland communities from northwestern Canada. It would be most instructive to study stands between these and the grasslands far to the southeast. The soils in these stands were usually well developed, permafrost was absent to the depths dug, soil reaction was alkaline to mildly acid, and effervescence often occurred upon application of 20% HCl. The root systems were well developed and penetrated deeply. They show much resemblance to associations in Norway in Nordhagen's *Veronica fruticans-Poa glauca* Alliance in the Order comprising rubble-slide plant communities (1943).

STAND 61 CALAMAGROSTIS PURPURESCENS-ARTEMISIA FRIGIDA

This community covered fairly extensive areas between low thickets of mostly aspen with scattered white spruce on steep, 35°-40°, southfacing slopes in the upper Matanuska River Valley near the Matanuska Glacier, at an elevation of about 3000 feet, near Mile 94 from Anchorage. This stand was studied on July 21, 1949. The plant cover was rather open, 749 hits, 61% *Calamagrostis purpurescens*, and 20% *Artemisia frigida*. The bunches of *C. purpurescens* were about 1 foot in diameter, 1 to 4 feet apart, and covered with dry straw on the downhill side. The leaves were about 15 inches high and the inflorescences reached 30 inches. Between the grass clumps were scattered plants of *Artemisia frigida*, 8 to 12 inches high, *Potentilla pennsylvanica* in bloom at 12 to 16 inches, *Bromus pumpellianus, Artemisia dracunculoides, Antennaria oxyphylla, Cladonia* sp., etc. (Table 7). Only 17 species were listed in this stand, 9 of which were hit.

Lichens were fairly well distributed over the surface, with scattered cobbles and gravel pebbles. Occasionally tree roots were exposed and in places slight erosion due to runoff had occurred. A crust about 0.25 inch thick had formed under some of the lichens.

Outstanding features of the soil profile were 1) the well developed silt loam to 13 inches, 2) the great thickness of the shale-like particles between 13 and

35 inches, mixed with silt in the upper part, 3) the lime-incrusted shale rocks, mixed with shale gravel at 35-40 inches, 4) the well compacted and partly cemented shale at 40 inches, 5) the large number of roots to the working depth at 40 inches, 6) the dryness of the soil due to its porosity and the very steep slope, 7) alkaline reaction, pH 7.4-7.8.

STAND 62 ARTEMISIA FRIGIDA-BROMUS PUMPELLIANUS

This stand, located near Mile 83 from Anchorage, elevation about 2000 feet, on a steep south-facing slope of 25°-30° in the upper Matanuska Valley. It was an earlier stage in succession than the preceding stand, as indicated by the more gravelly soil, the open cover, and the greater abundance of *Artemisia frigida,* which constituted 30% of the cover. The areas occupied by this community between aspen thickets were fairly small (Fig. 26). The total number of species was 16, of which 10 were hit. The total number of hits was only 384. After *Artemsia frigida* the most abundant vascular species were *Bromus pumpellianus, Artemisia dracunculoides, Rosa acicularis, Potentilla pennsylvanica, Calamagrostis purpurescens,* and *Poa glauca.* A few grasshoppers about 1 inch long were also seen. The stand was studied on July 22, 1949.

On the surface were scattered leaves and stems, a few rabbit pellets, dead Juniperus stems, and lichens formed a crust 0.25-inch thick in spots. Outstanding features of the soil profile were 1) silt loam with shale fragments to 3 inches, gravelly shale with little silt and sand at 3-32.5 inches, sand with some gravel and boulders at 32.5-45 inches (see Fig. 27), 2) penetration and seepage of water occurs readily, 3) roots very numerous to 23 inches, working depth at 33 inches, 4) soil less developed than in the preceding stand, 5) reaction neutral to slightly acid, pH 6.2-7.2, 6) no effervescence with 20% HCl.

STAND 63 POA GLAUCA-ARTEMISIA FRIGIDA-CALAMAGROSTIS PURPURESCENS

This stand was a short distance lower on the

FIG. 26. *Artemisia frigida-Bromus pumpellianus* community (Stand 62) at 2000 feet in the upper Matanuska Valley, northeast of Palmer. Aspen in the background. July 22, 1949.

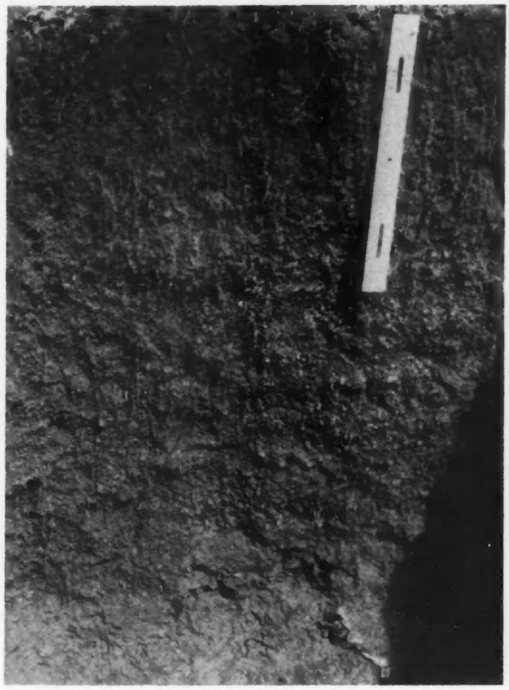

FIG. 27. Soil profile in *Artemisia frigida-Bromus pumpellianus* community (Stand 62, see Fig. 26) with very numerous roots to 23 inches and working depth at 33 inches, in loose, gravelly, brown material. July 22, 1949.

same steep slope of about 40° on which the preceding stand was located. It appeared to be intermediate in succession between the 2 preceding stands, as indicated by the cover of 679 hits, which was somewhat more open than Stand 61, by the plant composition, and the intermediate status of the soil development. *Poa glauca* made up 27% of the cover, *Artemisia frigida* 23%, *Calamagrostis purpurescens* 17%, and *Bromus pumpellianus* 11%. The inflorescences of the grasses reached 2 to 3 feet in height, the leaves 1 to 2 feet. Other prominent species were *Rosa acicularis* 12 to 15 inches high, *Artemisia dracunculoides, Potentilla pennsylvanica,* and small, scattered living and dead aspens. The total number of vascular species was only 13, of which 10 were hit.

On the surface grass straw was scattered thinly, especially on the down-slope sides of grass tufts, the accumulation of several years. Lichens occurred in open spots, binding the soil into blocks about 0.25 inch thick. Outstanding features of the soil profile were 1) the numerous fine roots to 32 inches, 2) the large amount of gravel and rock in the soil in relation to the cover of vegetation in the silt loam at 2.5-15.5 inches, 3) the well developed 0-2.5-inch horizon of silt loam, 4) reaction pH 7.4 in the surface horizon, 6.0 at 10 inches, 5) effervescence of the white coatings on rocks in the silty gravel at 15.5-32 inches,

6) absence of shale gravel, which occurred in the two preceding stands.

STAND 65 AGROPYRON SPICATUM-ARTEMISIA FRIGIDA

This grassland community, dominated by *Agropyron spicatum,* chiefly, was found on some widely separated, very steep slopes, 30° to 45°, facing the southeast, along the Tanana River, about 75 miles east of Fairbanks. The steep grassland areas were conspicuous at a considerable distance because they formed islands in the forest of white spruce, birch, aspen, willows, etc., which occurred on the tops and less steep portions of the hills. In the stand selected for study (Fig. 28) on August 4, 1949, was a U. S. Cadastral Survey stake labelled T7S, S34/R8E, S35/1949. The cover was moderately dense, 1212 hits, composed of 61% *Agropyron,* in loose bunches with inflorescences 2.5 to 3 feet tall, 16% *Artemisia frigida* 4 to 6 inches, *Poa glauca* 2 feet, *Anemone patens multifida, Rosa acicularis* 1 foot, *Erigeron* sp. 8 to 10 inches, *Calamagrostis purpurescens,* and a few more (see Table 7), making a total of 14 vascular species, of which 12 were hit. It is noteworthy that *Agropyron spicatum* occurred in abundance in the Tanana River Valley, but was not seen in the upper Matanuska River Valley farther south, and that *Poa glauca* and *Calamagrostis purpurescens* were found in both. This stand appeared from the soil profile (Fig. 29) to be an old grassland. This community may have been more extensive during an earlier, warmer geological period.

Outstanding features of the soil profile were 1) the great depth to which dark silt loam occurred, to 41 inches, gravel and rocks increased with depth so that digging was difficult below 31 inches, 2) roots numerous to working depth at 41 inches, maximum below 43.5 inches, 3) the compact silt loam at 0.4-3 inches, 4) much lime incrustation in rocky layers below 10.5 inches, alkaline reaction throughout, pH 7.4-8.0, 5) a well developed profile indicating an old grassland stand, 6) mosses and lichens formed a very thin layer over the surface between other plants.

FIG. 28. *Agropyron spicatum-Artemisia frigida* community (Stand 65) on bank of Tanana River, about 75 miles east of Fairbanks. An old grassland stand. Aspens scattered on part of the slope. August 4, 1949.

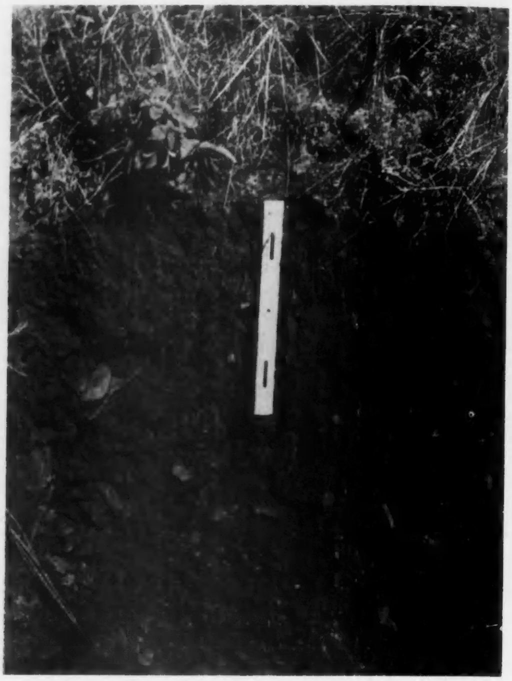

FIG. 29. Soil profile in *Agropyron spicatum-Artemisia frigida* community (Stand 65, see Fig. 28). Dark soil to depth of 41 inches, the working depth of the roots. Lime incrustations on rocks below 10.5 inches, alkaline reaction, pH 7.4-8.0, throughout. August 4, 1949.

STAND 77 ELYMUS INNOVATUS-POA GLAUCA

Communities dominated by *Elymus innovatus-Poa glauca,* and by *Poa glauca-Calamagrostis purpurescens,* located on many steep slopes, 30° to 45°, facing south and southwest, at about 1500 feet elevation occur across the Nenana River, and along the Healy River, east of the railway station of Healy, north of the Alaska Range. Stands were studied here on August 19, 1949, and again in 1950. The latter type of community was on more gravelly areas, it was more open, and apparently in an earlier stage in succession than the former. They resembled communities in the upper part of the Matanuska River Valley, represented by Stands 61, 62, and 63. These communities occurred in large and small openings between stands of trees such as balsam poplar, aspen, white spruce, willows and alders. In places on these steep slopes gravel slides had occurred recently.

A stand of the *Poa glauca-Calamagrostis purpurescens* on a 45° west-facing slope on the east side of the Nenana River contained in addition to the 2 dominants the following species; abundant; *Elymus innovatus, Oxytropis gracilis,* and *Draba aurea;* moderately abundant, *Silene repens, Galium boreale,* and

FIG. 30. Stand 77. *Elymus innovatus-Poa glauca* community, balsam poplar beyond the grassland, white spruce on the bench below, and willows on the bottomland where the Healy River joins the Nenana River. Healy is located on the first bench beyond the Nenana River, August 19, 1949.

Carex supina; scattered, *Plantago canescens, Silene williamsii, Saxifraga tricuspidata, S. nivalis,* and *Potentilla virgulata.*

The stand selected for detailed study in the *Elymus innovatus-Poa glauca* community, on August 19, 1949, was on a 40-50° south-facing slope. The cover was moderate, 1020 hits (Fig. 30), of which *Elymus* made up 51%, *Poa glauca* 14%, and *Anemone ludoviciana* 10% (Table 7). The leaves of *Elymus* were 10 to 14 inches high, the inflorescences 22 to 26 inches. Other prominent species were *Rosa acicularis, Plantago canescens, Carex supina, and Galium boreale. Calamagrostis purpurescens* occupied only about 1% of the cover. The total number of vascular species was 21, all hit. Dead leaves were scattered on the surface and in spots formed a loose layer about 2 inches thick, in which foliose lichens and moss occurred sparsely.

Outstanding features of the soil profile were 1) the abundance and the unusually great depth of the roots, working depth at about 90 inches (Fig. 31), 2) uniformity of the profile, silt loam horizons to the gravel and sand below 90 inches, 3) acid reaction throughout, pH 5.8-6.8, 4) an old grassland as indicated by the deep soil development, 5) no effervescence.

STAND 64 FESTUCA RUBRA-CAREX SUPINA-AGROPYRON LATIGLUME

This very interesting community occurred as moist meadows at an elevation of about 1900 feet on nearly flat land on the first bench above the Delta River, near Donnelly, south of the junction with the Tanana River. It occupied fairly large areas between thickets of willows and occasional white spruces. The vegetation was dense, forming usually a thick soft carpet. The stand selected for detailed study on August 3, 1949, had good cover, 1341 hits, consisting of 50% *Festuca rubra,* inflorescences 2 feet high, 11% *Carex supina,* and 10% *Agropyron latiglume.* As shown

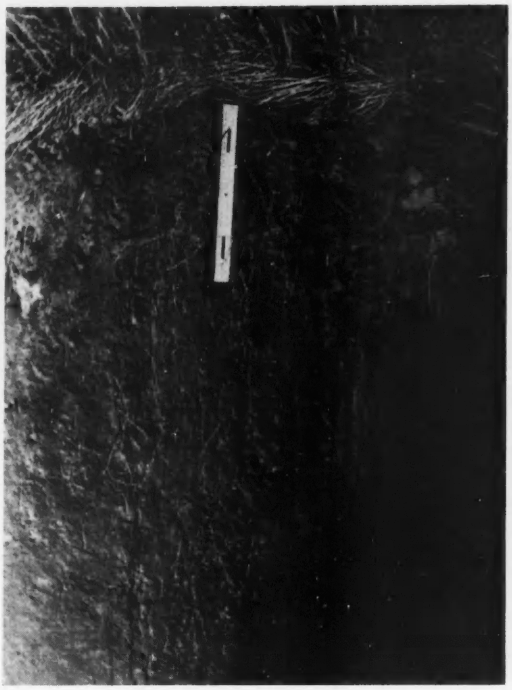

FIG. 31. Soil profile in the *Elymus innovatus-Poa glauca* community (Stand 77, see Fig. 30). Remarkably deep working depth of the roots at 90 inches. Granular silt loam very uniform to about 90 inches, pH 5.8 to 6.8 August 19, 1949.

in Table 7, other important species were *Bupleuron americanum,* its yellow flowers conspicuous at a height of 8 inches, *Oxytropis gracilis* and *Astragalus alpinus* with flower spikes about a foot high, *Linum lewisii* blooming at 10-12 inches, *Zygadenus elegans, Epilobium angustifolium, Poa pratensis,* and *P. alpina,* about 15 inches high. The general height of the foliage was 7 to 12 inches. Relationship to the preceding 5 stands in this group is indicated by the presence of *Elymus innovatus, Carex supina, Calamagrostis purpurescens, Arenaria lateriflora,* and *Saxifraga reflexa.* The total number of species in this stand was 25, 14 hit. Mosses formed scattered hummocks about an inch high, and a layer 2 to 3 inches thick in depressions.

Outstanding features of the soil profile were 1) the well developed dark, fibrous, silt-loam horizon at 0-2 inches, 2) dark colored silty fine sand to 4.75 inches, then sandy gravel to 7.25 inches and sandy gravel with many cobbles to 20.25 inches, 3) gravel with many stones at 20.25-30 inches, 4) large number of roots to working depth at 22 inches, maximum 29 inches, 5) reaction pH 6.6-5.0 to 7.25 inches, below that pH 7.4, effervescence only below 7.25 inches.

DISCUSSION OF GRASSLAND COMMUNITIES ON THE UPLANDS

The Cliff Meadow communities, near the edges of

cliffs on Kodiak Island were especially well developed, containing 47 and 36 species in the two stands that were studied. The dominant species were *Deschampsia beringensis, Poa glauca, Carex macrochaeta, Calamagrostis canadensis,* and some forbs. The soil was deep and of excellent structure, the working depths of the root systems were at 16-19 inches, maximum depths at 33-41 inches.

The Tall Grass-Forb with *Calamagrostis canadensis* as the Chief Dominant communities cover great areas in Alaska, in the open or as a layer in forest which is not dense. Some of the chief forbs are *Epilobium angustifolium, Heracleum lanatum, Angelica* spp., *Geranium erianthum, Sanguisorba sitchensis,* and several tall ferns. Usually there is a thick inflammable layer of straw on the surface, the soil is fairly deep and fertile, often with much organic material in the upper horizons, and rocky or gravelly in the lower layers, usually very good root development with working depths at 23 to 35 inches and maximum depths at 29 to 44 inches, except higher in the mountains where they were more shallow.

The Medium Tall Grass-Forb with *Festuca altaica* as the Chief Dominant communities are also widely distributed. Floristically it is similar to the second group, except that *F. altaica* is the chief dominant. Many forb species are common to both groups. The soil is usually deep and well developed, the working depths of the root systems are at 17 to 31.5 inches, maximum depths at 24 to 32 inches. Stands of this and the preceding communities are often small due to variations in the substratum.

The *Agropyron trachycaulum* communities, located in the Matanuska Valley, were fairly open, located on steep south-facing slopes with farily well developed, deep, porous soil. Associated forbs were similar to those in the two preceding groups. The roots penetrated very deeply, working depths at 38-44.5 inches, maximum depths at 47-60 inches.

The Miscellaneous Upland Grassland communities were represented by 5 stands on steep, south-facing slopes in interior Alaska. They resembled one another by the presence of species which were common to 4 or 5 of them, such as *Calamagrostis purpurescens, Poa glauca, Potentilla pennsylvanica, Rosa acicularis, Galium boreale,* and *Artemisia frigida.* These 5 communities appear to be outliers of grasslands far to the southeast. The soils were of loose structure and usually fairly well developed. The root systems were well developed and penetrated very deeply, working depths at 32-90 inches. The sixth stand was a mountain meadow along the Delta River, in which *Festuca rubra, Carex supina,* and *Agropyron latiglume* were the dominants. A number of forbs were characteristic of this stand, such as *Bupleuron americanum* and *Linum lewisii.* The shallow, silt loam, surface soil was underlaid by sand and gravel strata. The root systems were rather shallow, working depth at 22 inches, maximum at 29 inches.

SHRUB AND FOREST COMMUNITIES

The vegetation and the soil profiles in a few shrub and forest communities were studied primarily for comparison with the grassland communities. Some of the chief species forming these communities are alders, willows, birches, drawf heath shrubs, sweet gale, elderberry, salmon berry, wild currant, raspberry, silverberry, soapberry, buffalo berry, highbush cranberry, rose, spiraea, juniper, aspen, poplars, Sitka spruce, white spruce, black spruce, and tamarack. Many communities have only one species as a dominant, others have two or more, such as the Alaska birch-white spruce community which covers wide areas in interior Alaska. Much research is needed in order to adequately characterize these numerous communities. Much of the herbaceous vegetation in the open shrub and tree communities resemble Nordhagen's (1943) tall herb mountain meadow communities in the order *Aconitetalia* in Norway. Hustich (1949) made a preliminary classification of forest types in Labrador and compared them with types in some other parts of the boreal forest region.

STAND 28 ALNUS FRUTICOSA

Alder communities of this and other species are widespread in many parts of Alaska. Some kinds occupy extensive areas on mountain slopes above timber line, on newly exposed terrain uncovered by retreating glaciers, etc. This stand, studied on July 2, 1949, was representative of the alder community which covers much ground in the northeastern part of Kodiak Island and probably other parts of the island which were not seen. It was a thicket 3 to 4 rods wide and somewhat longer, in a shallow draw, surrounded by mixed shrubby and fragmentary grassland communities, on the north-facing slope of about 15°, at an elevation of about 800 feet on the divide between the Naval Air Station and Anton Larsen Bay. The alder stems extended along the ground downhill for several feet, then gradually ascended diagonally upward to about 10 feet in height. This type of growth was undoubtedly due to snowslides and the weight of snow drifts. The stems near the ground were 4 to 5 inches in diameter, forming an almost impassable network. *Rubus spectabilis* was very abundant in a distinct layer at 30-36 inches. Mixed with it were *Sambucus pubens,* 30 to 36 inches high, *Dryopteris austriaca,* 12 to 30 inches, *Calamagrostis canadensis,* 6-24 inches in the more open spots, *Stellaria sitchana,* and *Deschampsia beringensis.*

Outstanding features of the soil profile were 1) the numerous roots on the surface and under the 1-inch layer of leaf mulch and moss, 2) the stratified ash layer only 10 inches thick below the mucky organic layer at 0-0.5 inch, 3) surface horizon prior to the 1912 ash fall plainly marked at 10.5 inches by decaying vegetation in platy structure, 4) well developed soil below the ash at 10.5-23.5 inches where large rocks were encountered, 5) roots more numerous below the ash horizon than in it.

SCRUB BIRCH COMMUNITIES

The scrub birch species, *Betula glandulosa, B. nana exilis,* and hybrids between them and *Betula resinifera,* form communities with one of these species as the single dominant or with associated dominants over large areas of broad valleys and gentle slopes, above timber-line in the Alaska Range, on hillsides on Seward Peninsula, and elsewhere. According to Anderson (1943-1950), *B. glandulosa,* 1.5 to 4.5 feet tall, occurs in interior Alaska, while *B. nana exilis,* usually lower in height, occurs "nearly throughout Alaska." These communities resemble sociations in Norway classified by Nordhagen (1943) in the order; Dwarf Heath Shrub on Lime-poor Rock. They also resemble the "jernik" or "shrub tundra" of northern Siberia and in northwestern Manchuria (Imanishi 1950). Two stands are described below.

STAND 88 BETULA GLANDULOSA

This stand was located in the extensive area occupied by this community in Mt. McKinley National Park. Extensive areas of this community were seen also in the vicinity of Broad Pass. The stand, studied on August 26, 1949, was on a south-facing slope of less than 5°, about 8 miles west of the McKinley Park Railway Station, elevation about 3000 feet. The chief species were *Betula glandulosa,* 3 to 5 feet tall, *Empetrum nigrum, Vaccinium vitisidea, Carex bigelowii, Ledum decumbens, Salix pulchra,* and more scattered were *Cornus canadensis, Calamagrostis canadensis, Spiraea beauverdina, Petasites frigidus,* and occasionally a sapling of *Picea glauca.* Mosses and lichens formed a dense ground layer. The most common mosses were *Pleurozium schreberi* and *Polytrichum* sp. The most abundant lichens were *Cladonia rangiferina, Cladonia sylvatica,* and *Nephroma arcticum.* Moderately abundant were *Stereocaulon tomentosum, Cladonia amaurocraea, C. alpestris;* and sparse were *Cetraria islandica, C. cucullata, Cladonia gracilis chordalis, C. gracilis elongata, C. pleurota, C. gonecha,* and *Cetraria richardsonii.*

Important features of the soil profile were 1) the shallowness of the roots, mostly in the upper foot and especially in the upper 2.75 inches, working depth at only 16 inches, 2) high clay content between 4.75 and 17.5 inches and the highly impervious layer at 12 inches, 3) alternation of clay and sandy layers, 4) gray, leached layer at 2.75-4.75 inches, 5) acid reaction to depth of 21.5 inches, pH 4.4 to 4.6, 6) no effervescence.

Detailed description of the soil profile:

Mosses and lichens formed a layer 3 to 8 inches thick, the lower part fairly well decomposed.

0-2 inches. Dark reddish brown, fibrous and decomposed plant material, very little silt, very loose, roots very numerous, pH 4.4.

2-2.75 inches. Dark reddish brown, silt loam, a few rounded pebbles, picks out in thick plates which break into granules, roots very numerous, pH 4.6.

2.75-4.75 inches. Pinkish gray to light gray, reddish brown mottling in lower part of this and upper part of next horizon, fine sandy loam, occasional small pebbles, appears leached, picks out into small, loose granules, coarse roots numerous, fine roots scarce, pH 4.6, in some spots this horizon is lacking.

4.75-9 inches. Strong brown fine sand to yellowish brown fine sandy loam mottled with gray brown clay in a few spots, compact, picks out into sharply angled blocks up to 1 inch across, which crumble crisply into granules, roots numerous to scattered, pH 4.6.

9-17.5 inches. Variable, mostly clay, light yellowish brown, light brown gray, to dark brown, the latter with more sand and gravel, stratified, fissure planes in various directions, picks out in large blocks up to 5 inches across which break down into plates, roots scattered, pH 4.4 working depth of roots at 16 inches.

17.5-21.5 inches. Grayish brown, fine sandy clay, picks out in blocks which break down finally to single grains, roots scarce, pH 4.6

21.5-24.5 inches. Loose gravel with a little coarse sand, scattered cobbles up to 2 inches through, roots scarce to maximum depth at 22 inches, pH 6.0.

24.5-31 inches. Sand with some silt in upper part, sandy gravel layer below, and then sandy again with some silt.

STAND ANS BETULA NANA EXILIS-MOSSES-LICHENS

This stand was located on the east-facing slope of about 5°, elevation about 150 feet, on the west side of the Nome River about 10 miles northeast of Nome (Fig. 32). It was studied on June 30, 1950.

FIG. 32. A meter-square quadrat in the dwarf shrub-lichen community (Stand ANS), 10 miles northeast of Nome. Chief species are *Betula nana exilis, Vaccinium uliginosum, Ledum decumbens, Loiseleuria procumbens, Carex montanensis,* and lichens, 1 to 2 inches tall, including *Cladonia verticillata, C. rangiferina, C. sylvatica, C. gonecha, C. cornuta cylindrica, Cetraria cucullata.* June 28, 1950.

The shrubs were mostly *Betula nana exilis,* 2 to 4 feet tall, with intermixed *Salix pulchra* and *S. glauca* var. *acutifolia.* Openings between masses of shrubs varied from a foot to several yards across. The ground cover was complete, varying in composition from dense growth of lichens and mosses 1 to 2 inches high to short growth of scattered shrubs, sedges, and forbs. In the moister spots there was more sedge, in drier areas more lichen. On hummocks *Festuca altaica* formed small patches with lichens as a ground layer. Under the open shrubs and close to the larger ones lichens were often dense and 3 to 4 inches high. Under very dense shrubs, especially willows, mosses formed low mounds. This community is economically important for grazing by reindeer because of the large amount of lichen feed

that it produces. It resembles the *Betula nana-Empetrum nigrum-Cladonia alpestris* association in southern Norway described by Du Rietz (1925a).

The chief dwarf shrubs were *Vaccinium uliginosum* extending 4 to 8 inches above the moss and lichens, *Empetrum nigrum* 3 to 4 inches high, and the decumbent *Salix reticulata*, and *Rubus stellatus*. The following forbs were scattered: *Epilobium angustifolium, Claytonia sarmentosa, Senecio atropurpureus, Parrya nudicaulis, Dodecatheon frigidum, Papaver macounii, Cardamine pratensis, Pedicularis labrodorica, P. oederi, Thalictrum alpinum, Andromeda polifolia, Cerastium beeringianum, Saxifraga hieracifolia*, and *Lagotis stelleri*. The chief mosses were *Hylocomium splendens, Drepanocladus unicinatus, Polytrichum piliferum, Ptilidium ciliare*, and *Bryum* sp. *Selaginella selaginoides*, resembling a moss in form, was scattered. The chief lichens were *Cladonia rangiferina, C. sylvatica, C. cornuta cylindrica*, and *Cetraria cucullata*, which occurred in various microhabitats, including moss tufts. Other, less common species were *Cetraria islandica, Stereocaulon tomentosum* (also on moss), *Cladonia pleurota, C. macilenta, C. delessertii, C. verticillata, C. gonecha, Sphaerophorus globosus, Ochrolechia frigida, Pertusaria coccodes, Pilophorus cereolus, Thamnolia vermicularis*, and *Nephroma arcticum*.

Detailed description of the soil profile:

The irregular hummocky surface has been influenced by frost action and solifluction (Hopkins & Sigafoos 1951, Hanson 1950b).

0-2.5 or 3.0 inches. Dark reddish brown, silt loam mostly decomposing organic matter and some gritty material, wet, occasional 1-to 2-inch rocks, roots very numerous, pH 5.0.

2.5 or 3 to 8.5 or 9 inches. Variable, brown to dark brown silt, saturated, water with silt oozes along vertical surfaces, jellylike, parts were ready to flow, a "fliesserde" massive, occasional streaks of olive gray silt, roots very numerous,, pH 4.8.

8.5 or 9 to 11 or 12 inches. Dark yellowish brown silt, with occasional pebbles, structures similar to above, wet, roots numerous, frozen at 11 to 12 inches, pH 4.8.

Willow Communities

Willow communities are common along streams, lakes, marshes, draws, etc., in Alaska. Many species including tall tree-like forms in the more southern parts to low trailing kinds in alpine and arctic situations may occur as dominants or codominants. More attention was given in this study to willow communities on the Seward Peninsula in the vicinity of Nome than elsewhere. Two chief kinds of communities of the taller willows were distinguished; *Salix alaxensis*, and *S. richardsonii-S. pulchra* communities, but undoubtedly additional kinds occur, particularly if the ground flora and soil conditions are considered in greater detail.

The *Salix alaxensis* community formed a grayish green zone along streams, such as the Nome and Snake rivers, and as small clumps on the borders of very small streams. The soil was usually well-drained, coarse gravel occurring close to the surface. The zone varied considerably in width, and under suitable conditions was several rods wide. Balsam poplar (*Populus tacamahacca*) was often scattered in it. The height of trees was about 15 feet. The color makes it conspicuous from the air.

The *Salix richardsonii-S. pulchra* community, green or slightly yellowish green in color, was often found between the preceding zone and the steeply ascending bank of the flood plains, or between the preceding zone and the sedge marsh on poorly drained land next to the bank. Balsam poplars occurred sparsely. The general height was 4 to 8 feet. The soil was usually rather poorly drained. The stand was fairly open, with sedge marsh between the willow clumps, and occasionally water in the depressions. This community also occurred as irregular stands in shallow draws on slopes, in which small streamlets were often seen. When the snow is melting in the spring most of the draws apparently contain much running water, especially in the irregular channels between hummocks, which are as much as 2 to 3 feet high. These willows were up to 10 feet tall and formed dense thickets in places. The vegetation on the hummocks was somewhat different from that of the depressions, so this community might be considered a mosaic of microcommunities.

A stand, studied on July 1, 1950, on the east-facing slope above the Nome River, about 10 miles northeast of Nome, elevation about 200 feet, contained the following species on hummocks: chiefly *Calamagrostis canadensis, Festuca altaica, Carex aquatilis, Rumex arcticus, Sedum roseum, Carex nesophila, Iris setosa, Vaccinium uliginosum, Anemone narcissiflora, Galium boreale, Empetrum nigrum, Salix reticulata, Andromeda polifolia, Artemisia arctica, Dryas octopetala, Equisetum arvense, Mertensia paniculata, Viola langsdorfii, Luzula multiflora*, and mosses, chiefly *Polytrichum piliferum, Hylocomium splendens, Drepanocladus uncinatus*. On the lower sides of the hummocks and in the depression were *Carex aquatilis, C. lugens, C. vaginata, Dodecatheon frigidum, Woodsia glabella, Ranunculus pedatifidus, Sedum roseum, Potentilla fruticosa, Salix reticulata, Primula parvifolia, Corydalis pauciflora, Equisetum arvense, Pedicularis capitata, P. arctica*, and the mosses: *Bryum* sp., *Ptilidium ciliare*, and those named above on the hummocks.

The two soil profiles examined in this stand differed considerably. In one, under a hummock close to the edge of a drainage channel, frozen ground was not encountered to depth of 38 inches (as deep as dug), while in the other, a broad, flat area under a willow, only a foot away, the ground was frozen at only 9 inches. This difference was probably due to the shading by the willow and to the warming influcnce of the drainage water that had flowed earlier. Silt loam extended to a depth of about 17 inches, below that was silt or sandy silt with gravel and scattered stones.

SPRUCE COMMUNITIES

The vegetation and soil profiles were studied in two *Picea sitchensis* communities, one on Kodiak Island, the other near Homer, and one *Picea glauca* community, near Palmer.

STAND 2 PICEA SITCHENSIS

This stand, located on Miller's Point, Kodiak Island, consisted of trees about 65 to 70 feet tall, and trees of average diameter were about 115 years old, as determined by increment boring on July 4, 1949. The stand varied considerably in density. In a 50 x 50 foot plot, in which the point-contact method was used for the ground vegetation and the soil profile description made, there were 21 live *Picea sitchensis* trees (circumference at 3.5 feet high 15 to 82 inches) and 24 dead trees which had been suppressed. In the denser parts of the forest there was very little ground vegetation, except a thick layer of mosses and a few scattered plants, especially *Rubus pedatus* and *Dryopteris disjuncta*. In the more open places *Rubus spectabilis* and *Oplopanax horridus* were usually abundant, and associated with them in less abundance were *Dryopteris disjuncta*, *D. austriaca*, and *Equisetum arvense*. The total number of hits was only 247, of which the mosses, chiefly *Hylocomium splendens* and *Rhytidiadelphus* sp. received 200.

Outstanding features of the soil profile were 1) the 2- to 3-inch thick carpet of moss with the 1- to 2-inch layer of decaying plant debris below, 2) the stratified ash layer, 9.75 inches thick, showing apparently little change since 1912, due possibly to the few roots in it, 3) the former surface horizon at 9.75-11.75 inches, consisting of mucky material and partly decayed pieces of needles, twigs, etc., 4) dark, well developed clay loam with slate and argillite fragments at 11.75-14 inches, 5) rock and gravel at only 14 inches, mixed with fine sandy loam or clay, 6) scarcity of roots in the ash and the uniform and thorough distribution below the ash to 26.5 inches.

STAND 34 PICEA SITCHENSIS

This stand was located on a 5° to 10° slope, facing northeast, about 6.5 miles northwest of Homer, about 200 feet above sea-level. The trees were about 60 to 75 feet high. There was much down timber so it was difficult to walk in it. Some seepage was occurring. The stand was fairly open, and the following species were found in it on July 6, 1949.

Commonly occurring species were *Alnus fruticosa sinuata, Equisetum arvense, Calamagrostis canadensis, Dryopteris austriaca, D. disjuncta, Rubus pedatus,* and *Equisetum sylvaticum*. More scattered were *Menziesia ferruginea, Betula resinifera, Spiraea beauverdiana, Empetrum nigrum, Linnaea borealis, Cornus suecica, Rubus chamaemorus,* and others, making a total of 27 vascular species.

Outstanding features of the soil profile were 1) the large quantity of organic matter in sandy silt to a depth of 27 inches, 2) numerous roots to 27 inches, 3) the high soil moisture content, 4) absence of rocks above 24.75 inches.

STAND 46 PICEA GLAUCA

This stand was part of the forest on the almost level bench along the Matanuska River, about 6 miles southwest of Palmer. On July 20, 1949, the dense forest was composed of *Picea glauca* and *Betula resinifera*, reaching elevations of about 60 feet. There were more birch trees than spruce, but the latter were taller and greater in diameter. Much of the spruce in similar stands had been cut for lumber and some of the land cleared for cultivation. Most of the ground was shaded so the vegetation beneath the tree canopies was sparse. There were only 389 hits, of which *Hylocomium splendens* received 158. This moss was also the chief ground species in the Sitka spruce forest on Kodiak Island. *Rhytidiadelphus*, also occurred in both forests. The mosses, interspersed with plant debris, were usually 1 to 2 inches thick, but up to 4 to 5 inches on top of decaying logs. The most prominent vascular species were *Dryopteris disjuncta* and *Linnaea borealis*, the former also in the Kodiak forest. There were 22 species in the stand, only 12 of which were hit. This number included some species which are more characteristic of grasslands, such as *Calamagrostis canadensis*, *Epilobium angustifolium*, *Rosa acicularis*, and *Equisetum pratense*. This stand showed resemblance to Osvald's *Picea excelsa* associations in the Komosse Region in Sweden (1923).

Outstanding features of the soil profile were 1) roots numerous to only 8.5 inches, shallow working depth at 18 inches, maximum 37.5 inches, 2) large quantity of decaying plant debris on the surface, 3) the podsolized silt-loam horizon at 0-3.5 inches, which contained most of the larger tree roots, 4) mottled silt loam at 3.5-6 inches, 5) much variation in the 6-26-inch horizon, composed of silt with ash and charred wood, 6) silt with gravel at 26-30 inches, gravel and cobbles below, 7) pH 5.2-6.0.

STAND 44 BETULA RESINIFERA

Birch-spruce forest covers the greatest part of the Matanuska Valley. A stand, located about 8.5 miles north of Palmer on the Fishhook Road, on a southerly slope of less than 5° was selected for study on July 15, 1949. The elevation was about 800 feet. In a plot 50 feet square there were 9 *Betula resinifera* trees ranging from 3.4 to 16.2 inches in diameter at height of 3.5 feet and 5 dead trees. There were 29 *Picea glauca* trees, 1.8 to 5.7 inches in diameter and 4 dead trees. The tallest living birches were about 60 feet high, the spruces, none of which were thrifty, were 20 to 30 feet. An occasional dead spruce had reached a height of 70 feet. Most of the ground was shaded by the tree crowns but the light was not reduced so much as in the preceding white spruce stand, where the spruces were thrifty.

The vegetation beneath the tree canopies was fairly open, cover index of 1114 hits, made up chiefly of *Dryopteris disjuncta* and *Equisetum pratense*. Other prominent species were *Hylocomium splendens, Lycopodium annotinum, Cornus canadensis,* and *Pyrola*

TABLE 8

Species	Upland Marsh and Meadow Communities														Upland Bogs			
	Stand 76 Healy		Stand 52A Talk. Mts.		Stand 52B Talk. Mts.		Stand 84 McK. Park		Stand 81 McK. Park		Stand 85 McK. Park		Stand 67 Eag. Sum.		Stand 45 Wasilla		Stand 78 Healy	
	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %
Calamagrostis neglecta	738	100																
Calamagrostis canadensis			9	10											19	40	61	60
Festuca altaica			49	25														
Arctagrostis latifolia									7	5	x							
Trisetum spicatum									3	5								
Poa arctica													4	10			2	5
Poa sp.									8	15								
Deschampsia sp. ?									2	5								
Carex physocarpa	258	95			13	15												
Carex aquatilis	130	75					856	100							52	55		
Carex pluriflora			169	95	94	100												
Carex anthoxanthea			44	25														
Carex membranacea							3	5					276	40				
Carex bigelowii									605	95	277	70	315	90			333	95
Carex spectabilis									27	10								
Carex bipartita									1	5								
Carex rotundata											5	5						
Carex tenuiflora											x							
Carex vaginata													18	10				
Eriophorum angustifolium	75	50	263	95	259	100	14	30					30	45				
Eriophorum vaginatum											545	70	102	35				
Eleocharis aff. macrostachya	4	5																
Luzula multiflora									11	30								
Juncus albescens							2	5										
Scirpus caespitosus					38	20												
Equisetum arvense	7	10							103	70								
Equisetum palustre			55	75	41	80									1	5		
Equisetum alaskanum							100	90										
Equisetum variegatum									11	25								
Triglochin palustris	12	10																
Potentilla palustris	2	5													103	85		
Sanguisorba sitchensis			96	90														
Swertia perennis			30	55														
Thalictrum alpinum			42	50														
Erigeron peregrinus			16	10														
Sedum roseum			23	20					x									
Polygonum viviparum			12	25			1	5	12	25			7	20			1	5
Polygonum bistorta plumosum									15	35	1	5						
Viola adunca			10	20														
Valeriana capitata			9	15					7	20								
Menyanthes trifoliata			7	25	3	10												
Ranunculus lapponicus			4	15														
Ranunculus sulphureus									2	5								
Ranunculus sp.			2	10														
Pedicularis sudetica			3	5														
Pedicularis capitata									3	5			1	5				
Pedicularis labrodorica											1	5			9	20		
Aster sp.			3	5														
Caltha leptosepala			2	5														
Limnorchis dilatata			2	5														
Trientalis europaea arctica			2	5											3	10		
Anemone richardsonii			x						2	10								
Anemone parviflora									15	50								
Polemonium acutiflorum			x				x		4	15								
Parnassia palustris	x																	
Iris setosa interior	x																	
Iris setosa															x			
Hippuris vulgaris	x																	
Petasites frigidus									12	25							2	5
Cardamine purpurea									9	30								
Artemisia arctica									8	15								
Stellaria laeta									5	15								
Stellaria longipes													1	5				
Aconitum delphinifolium									3	15								
Dodecatheon frigidum									2	10								

TABLE 8—Continued

Species	Upland Marsh and Meadow Communities														Upland Bogs			
	Stand 76 Healy		Stand 52A Talk. Mts.		Stand 52B Talk. Mts.		Stand 84 McK. Park		Stand 81 McK. Park		Stand 85 McK. Park		Stand 67 Eag. Sum.		Stand 45 Wasilla		Stand 78 Healy	
	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %
Myosotis alpestris									5	10								
Boykinia richardsonii									2	5								
Saxifraga hieracifolia									x									
Saxifraga lyallii									x									
Claytonia sarmentosa									5	20								
Claytonia sp.									x									
Saussurea angustifolia									x									
Papaver sp.									x									
Tofieldia pusilla											5	10						
Senecio frigidus											x							
Lycopodium annotinum											x							
Pyrola secunda			2	5														
Pyrola grandiflora													2	10				
Potentilla fruticosa	x														x			
Salix richardsonii	7	10													x			
Salix niphoclada	x																	
Salix reticulata			118	100	2	5	1	5	36	60	3	5	13	35				
Salix fuscescens reducta			11	25	11	25									35	50		
Salix pulchra			x				20	40			x		7	5	11	15	46	25
Salix polaris									132	95								
Salix arctica													5	10				
Salix sp.			12	10											x			
Oxycoccus microcarpus			8	30							33	40			113	75		
Vaccinium vitisidea											59	50	13	50	11	5	74	50
Vaccinium uliginosum											63	60			17	15	140	65
Rubus stellatus			4	10														
Rubus chamaemorus											8	10	x		x		3	10
Andromeda polifolia			14	20	12	25					56	70			233	100		
Ledum decumbens											105	80	5	10			297	80
Empetrum nigrum											63	45						
Arctostaphylos alpina											3	5						
Betula nana exilis											25	30	x		197	90	290	95
Dryas integrifolia							1	5										
Dryas octopetala									38	25								
Dryas alaskensis													90	70				
Cassiope tetragona									7	5								
Seedling									1	5								
Hypnaceae spp.	200	100	200	100	200	100			x				140	70	1	5		
Polytrichum sp.											x							
Drepanocladus sp.							200	100										
Pleurozium schreberi											25	30			3	5		
Hylocomium splendens											11	10						
Aulocomnium palustre											7	15			115	85		
Dicranum sp.											6	15						
Camptothecium nitens															50	35		
Paludella squarrosa															9	15		
Sphagnum spp.											88	65			117	85	200	100
Lichens									x									
Cladonia rangiferina											40	55						
Cladonia sylvatica											1	5					x	
Cladonia alpestris											x							
Cetraria cucullata											33	65						
Cetraria islandica											7	20						
Thamnolia vermicularis											1	5						
Alectoria nigricans											x							
Alnus tenuifolius															x			
Myrica gale															226	95		
Equisetum fluviatile															81	85		
Chamaedaphne calyculata															53	60		
Picea mariana															8	10		
Drosera rotundifolia															x			
Spiranthes romanzoffiana															x			
Epilobium angustifolium																	2	5
No hits									5									
Total Number of hits	1433		1221		673		1198		1103		1471		1029		1467		1451	

spp. *Calamagrostis canadensis* was scattered. The total number of vascular species was 21 in addition to the 2 tree species, 16 species hit.

Outstanding features of the soil profile were 1) coarseness of the roots, up to 1 inch in diameter, and the large number of roots in the upper 5 inches, 2) the carpet-like, fibrous layer at 0-3 inches, 3) the 2-inch thick layer of decaying leaves on the surface and the large quantity of plant debris in the 0-3-inch horizon, 4) thickness of the gray 3-5.5-inch silt loam horizon showing podsolization, 5) considerable mottling of the silt loam at 5.5-11 inches, 6) silt with some sand at 11-18 inches, and below that gravel and cobbles with intermixed silt loam to sand and gravel farther down. 7) effect of organic matter apparent to below 22.5 inches, 8) shallowness of the roots, working depth at 19 inches, maximum 23.5 inches, 9) indications of former burns at 3 inches.

DISCUSSION OF SHRUB AND FOREST COMMUNITIES

These communities showed great differences in plant composition and in soil characteristics. As compared with grassland stands, the soil was more shallow, rocks were more numerous on or near the surface, the soil showed more podsolization, and the root systems were shallower. Permafrost was encountered at a depth of about a foot in the scrub birch stands in northwestern Alaska.

UPLAND MARSH AND MEADOW COMMUNITIES

Eight stands were studied and the soil profiles described, and a number of other areas were examined in this category. The floristic composition of five of these stands is given in Table 8. Six of these stands have been described by Hanson (1950a), so they are not described in detail in this paper. The stands previously described are: 52 A, *Eriophorum angustifolium-Carex pluriflora-Salix reticulata* on hummocks, and 52 B, *E. angustifolium-C. pluriflora* in depressions in the wet meadow in the Craigie Creek Valley in the Talkeetna Mountains; 67, *Carex bigelowii-C. membranacea* on Eagle Summit on the Steese Highway between Fairbanks and Circle; 81, *Carex bigelowii-Salix polaris* near Sable Pass in Mt. McKinley National Park; 85, *Eriophorum vaginatum-Carex bigelowii* at Wonder Lake in the Park; and 75, *E. vaginatum-C. bigelowii* on Baldwin Peninsula about 35 miles south of Kotzebue. These communities resemble the *Carex bigelowii-C. lachenalii* Sociation in the *Nardeto-Caricion* Alliance of Order C, Snow-field Communities of Nordhagen (1943) in Norway, which are considered valuable for grazing. Imanishi (1950) shows a similar *Carex* spp.-*Eriophorum vaginatum* tussock community in northeastern Manchuria. Two additional marsh communities, not previously described, are discussed below.

STAND 84 CAREX AQUATILIS

This stand was located in a portion of the marsh in the broad valley near Polychrome Pass in Mt. McKinley National Park on August 23, 1949. The elevation was about 3600 feet, and the land surface was nearly level. It was a short distance below the slope on which Stand 83, *Festuca altaica-Carex montanensis* was located. The chief species was *Carex aquatilis*, constituting 72% of the total plant cover, 1198 hits. The sedge plants were 12 to 15 inches high, growing in closely spaced tufts, with dead leaves, 6 to 8 inches tall intermixed with the green leaves. Mosses and other species, chiefly *Equisetum alaskanum* and *Salix pulchra*, 2 to 3 inches tall, occurred in openings between the tufts. There were only 10 vascular species in the stand, 9 of which were hit (Table 8). This community resembles associations in Norway in Nordhagen's (1943) Order IA, *Eutrophic-mesotrophic* Grass Marshes (*Caricetalia goodenowii*), Alliance *Caricion atrofuscae-saxatalis*.

Important features of the soil profile were 1) impervious clay layers alternating with seepage layers of sandy silt or sand, 2) clay layer and frozen ground at 24 inches impeding drainage, 3) material in various strata had evidently been washed in from higher ground nearby, 4) slight effervescence in the 0-1.5 horizon and below 13 inches, 5) reaction varied from pH 6.4 to 7.2, 6) shallow root systems with working depth at 22 inches, maximum at 24 inches.

STAND 76 CALAMAGROSTIS NEGLECTA-CAREX PHYSOCARPA-C. AQUATILIS

This very interesting community was in a small basin on the bench at an elevation of about 1800 feet, about 2 miles west of Healy above the Nenana River (Fig. 33). It was studied on August 18, 1949, and examined again in 1950. The basin was partly surrounded by *Populus tacamahacca* woods, with undergrowth and border of *Potentilla fruticosa, Salix* spp., and *Betula* spp. Water stands in this marsh during the forepart of the summer. The chief species making up the dense cover, 1433 points, were *Calamagrostis neglecta*, 50%, *Carex physocarpa*, and *C. aquatilis*, the 2 latter making up 28% of the cover. *Eriophorum angustifolium* was also a conspicuous species. As shown in Table 8, the total number of vascular species was 14, of which 9 were hit. This community resembles Nordhagen's (1943) subalpine *Nardus stricta* sociation in the Snowfield Communities Order (*Salicetalia herbaceae*). The illustration on p. 238 in Nordhagen of the basin in which snow drifts accumulate and in which water stands in early summer is very similar to the basin in which this stand was located. Regel (1947) stated that *Calamagrostis neglecta* made up the major portion of the weight of the hay cut in the *Calamagrostidetum neglectae* community in irrigated swamps in White Russia.

Outstanding features of the soil profile were 1) the thick layer of moss in many places, beneath the grasses and sedges, 12 to 15 inches high, 2) the peat horizon at 0-9 inches separated readily from the silt below, 3) alternation of and irregularities in the gray brown silt and dusky red peaty material at 9-33 inches, probably due to frost action (Hopkins & Sigafoos 1951), scattered rocks below 29 inches, 4)

FIG. 33. *Calamagrostis neglecta-Carex physocarpa-C. aquatilis* community (Stand 76) at elevation of about 1800 feet, 2 miles west of Healy. In the background, balsam poplar, willows, shrubby cinquelfoil, and birches. Soil profile showed peat to 9 inches with silt beneath. Working depth of roots at 18.5 inches, maximum 30.5 inches. August 18, 1949.

water seeped into the trench below the peat, due to the more impervious silt below, soil material washed out readily, 5) at 33-44 inches sandy to gravelly silt, 6) saturated throughout, peat was pressed down several inches by walking on surface, 7) roots numerous only near the surface, working depth at 18.5 inches, maximum 30.5 inches, 8) frozen ground not encountered to depth of 44 inches, as deep as dug.

DISCUSSION OF UPLAND MARSH AND MEADOW COMMUNITIES

The analyses in Table 8 show similarities and differences in 7 stands. Species occurring in 6 of the stands were *Eriophorum angustifolium* and *Salix reticulata;* in 4 stands *Carex bigelowii, Polygonum viviparum,* and *Salix pulchra.* The cover in these communities was fair to very good, ranging from 673 to 1471 hits, and usually the number of species was high. The root systems were usually shallow in the saturated substratum consisting of peat and silt. Frost action and solifluction were important soil factors.

UPLAND BOGS

This category includes stands in which Sphagnum was well developed and in which dwarf heath shrubs were numerous. Detailed studies were made in only two upland bogs, the first in the Matanuska Valley, the other near Healy. Species found in both bogs were *Sphagnum* spp., *Betula nana exilis, Vaccinium uliginosum, V. vitisidea, Rubus chamaemorus,* and *Salix pulchra.* The first had several kinds of moss and more vascular species than the second. The two stands are representative of two kinds of bog communities, which with other kinds, are widespread in Alaska (Dachnowski-Stokes 1941). Similarities and differences with marsh and meadow communities are readily apparent in Table 8. Dwarf heath shrubs are abundant in the bogs and in many of the marshes, sedges are usually more numerous in marshes, and Sphagnum more abundant in the bogs. The bog stands resemble Nordhagen's (1943) Association *Oxycoccus microcarpus-Empetrum hermaphroditum-Sphagnum* spp. which is widely distributed in Scandinavia. They also show resemblance to bogs on Mt. Washington in New Hampshire described briefly by Antevs (1932), to those in Labrador described by Wenner (1947), to some in Russia described by Regel (1947), and to some in the Fraser River Valley near Vancouver, B. C., described by Osvald (1923).

STAND 45 ANDROMEDA POLIFOLIA-MYRICA GALE-BETULA NANA EXILIS-SPHAGNUM-MOSSES

This bog was located in a narrow valley at the end of a small lake 4 or 5 miles southwest of Wasilla in the Matanuska Valley. The surface was very hummocky, and water stood in the depressions. It was necessary to select carefully places to stand so that one would not sink deep into the spongy mass. Black spruce was invading the borders. The point-contact frame was placed usually on the hummocks to make the frequency-cover determinations, shown in Table 8. In addition to the species named in the heading above, important species were *Potentilla palustris* which occurred mostly in water a foot or so deep, *Vaccinium oxycoccus,* and *Equisetum fluviatile.* The most abundant moss was *Aulocomium palustre.* The successional trend was indicated by the invasion in places of *Calamagrostis canadensis, Alnus tenuifolius,* and *Salix* spp. The total number of species was 25, of which 17 were hit, on July 18, 1949. The stand was noteworthy because of the large number of species having high frequency and cover. The cover was dense, 1467 hits.

STAND 78 CAREX BIGELOWII-BETULA NANA EXILIS-LEDUM DECUMBENS-SPHAGNUM

This stand was situated on a north-facing slope of less than 5°, at an elevation of about 2600 feet, approximately 5.5 miles west of Healy. The cover was dense, as shown by the total number of 1451 hits. There were only 13 vascular species, of which 12 were hit (Table 8). In addition to the species named in the heading the following were conspicuous; *Vaccinium uliginosum, V. vitisidea, Calamagrostis canadensis langsdorfii,* and *Salix pulchra.* It differed from the preceding stand in the absence of other mosses and the greater abundance of Sphagnum, the thick layer of Sphagnum, up to 12 inches in hummocks, fewer species, the shallowness of the frozen ground, evidence of solifluction (Hanson 1950b, p. 622), etc. The soil profile consisted of peat for 5 inches beneath the Sphagnum, then 5 inches of slightly sticky silt which had a layer of peat in it, and frozen ground at 10 inches. Roots were numerous to the frozen ground.

DRYAS COMMUNITIES

In this category are placed a number of stands in which *Dryas integrifolia, D. octopetala,* or *D. alaskensis* is the chief, or one of the chief dominants.

TABLE 9

Species	Dryas Communities						Luetkia Pectinata Communities			
	Stand 86 McK. Park		Stand 82 McK. Park		Stand 66 Eagle Sum.		Stand 53 Talk. Mts.		Stand 54 Talk. Mts.	
	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %
Festuca rubra	152	80	27	25						
Festuca altaica	14	5	13	10						
Festuca brachyphylla			x		x					
Poa alpina			6	10						
Poa arctica					2	10				
Poa sp.	1	5					1	5	5	20
Arctagrostis latifolia			23	30						
Arctagrostis arundinacea	x									
Calamagrostis purpurescens			2	5						
Trisetum spicatum			x							
Hierochloe alpina					5	15				
Kobresia myosuroides			281	85						
Carex capillaris	8	20			23	15				
Carex scirpoidea	x		73	75	4	5				
Carex capitata	x									
Carex media	x									
Carex membranacea			x		3	15				
Carex misandra					138	50				
Carex bigelowii					127	55				
Carex vaginata					5	5				
Carex rupestris					1	5				
Carex sp.					3	10	4	20	3	10
Luzula confusa					6	15				
Luzula multiflora					x					
Luzula sp.			3	10					x	
Juncus arcticus	x									
Equisetum variegatum	74	55								
Equisetum arvense			77	55						
Epilobium angustifolium	9	10								
Epilobium latifolium	1	5								
Anemone parviflora	2	10	3	15						
Gentiana prostrata	1	5								
Gentiana propinqua			1	5						
Pedicularis sudetica	x									
Pedicularis capitata			7	30	3	5				
Pedicularis langsdorfii					5	15				
Polygonum viviparum	x		14	50	8	30				
Polygonum bistorta plumosum					x					
Parnassia palustris	x									
Aster sibiricus	x									
Hedysarum alpinum americanum	136	90	129	90						
Oxytropis viscidula			20	55						
Oxytropis scammaniana					23	15				
Stellaria longipes			6	20						
Tofieldia coccinea			2	5	3	5				
Tofieldia pusilla					x					
Saussurea angustifolia			1	5	1	5				
Cardamine purpurea			1	5	x					
Myosotis alpestris			x							
Eretrichium aretioides					8	15				
Arenaria rossii					3	5				
Papaver macounii					1	5				
Silene acaulis					2	5				
Eutrema edwardsii					x					
Saxifraga punctata					x					
Seedling			3	15						
Dryas integrifolia	506	100	67	35						
Dryas octopetala			316	95	136	40				
Dryas alaskensis					133	70				
Salix reticulata	41	60	36	65	2	10				
Salix pulchra	x									
Salix alaxensis	x									
Salix arbusculoides	x									

TABLE 9—Continued

Species	Dryas Communities						Luetkia Pectinata Communities			
	Stand 86 McK. Park		Stand 82 McK. Park		Stand 66 Eagle Sum.		Stand 53 Talk. Mts.		Stand 54 Talk. Mts.	
	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %	Hits	Freq. %
Salix richardsonii	x									
Salix arctica			53	60	16	40				
Potentilla fruticosa	1	5	x							
Vaccinium uliginosum			1	5	29	45				
Vaccinium vitisidea					6	15				
Arctostaphylos rubra			24	15						
Arctostaphylos alpina					1	5				
Cassiope tetragona					8	5				
Rhododendron lapponicum					1	5				
Empetrum nigrum					x		1	5	1	5
Rubus chamaemorus							1	5		
Rubus stellatus							x			
Luetkia pectinata							162	100	86	100
Cassiope stellarianum							125	100	11	35
Lycopodium alpinum							112	100	67	85
Lycopodium selago							1	5		
Salix polaris selwynensis							11	30	5	15
Listera cordata							2	5		
Ranunculus occidentalis									x	
Claytonia sarmentosa							x			
Dicranum sp.							56	65	27	60
Polytrichum sp.									2	10
Mosses	x				x					
Dactylina arctica					2	10				
Cetraria sp.					1	5				
Cetraria islandica?							8	25	7	25
Cladonia gracilis							10	35	49	90
Cladonia bellidiflora							5	15	52	85
Cladonia rangiferina									8	10
Cladonia alpestris?									9	5
Cladonia silvatica?									7	10
Cladonia sp.							2	5	15	40
Cladonia sp.									2	5
Lobaria sp.							3	15	30	30
Peltigera aphthosa							2	5		
No hits	3		8		3				3	
Total number of hits	946	....	1189	....	709	....	506	....	386	..

These communities are widespread in Alpine and Arctic regions in Alaska. The stands studied in detail were situated in Mt. McKinley National Park, on the hills north of Nome, and on a low raised beach in the vicinity of Kotzebue. These communities are similar to Nordhagen's (1927) "Artenreiche Dryas-Assoziation" in the group of Dwarf-shrub Communities Rich in Lichens and Mosses. Cooper (1931) points out the importance of species such as *Dryas drummondii, Epilobium latifolium, Rhacomitrium* spp., and *Salix* spp. in forming pioneer communities on the shores of Glacier Bay, following the retreat of glaciers. As shown in Table 9 some species common to all 3 stands were: *Carex scirpoidea, Polygonum viviparum,* and *Salix reticulata.*

STAND 86 DRYAS INTEGRIFOLIA-HEDYSARUM ALPINUM AMERICANUM-FESTUCA RUBRA

This community was located between the willows

on the flood plain of the Savage River at an elevation of about 2500 feet, approximately 7 miles west of McKinley Park railway station. It provides good grazing for moose, and grizzly bears dig out and eat the Hedysarum roots (Murie 1949). On August 26, 1949, *Dryas integrifolia* made up 53% of the medium extent of cover, 946 hits. In addition to the species named above, conspicuous species were *Equisetum variegatum* and *Salix reticulata.* The total number of vascular species was 26, of which 13 were hit.

Beneath the fairly dense Dryas plants with leaves up to 3 inches high and flowers to 7 inches, the ground was covered with a layer of dead leaves and stems about 0.75 inch thick, in which small snail shells were scattered. Features of the soil profile were 1) below the 0-0.75-inch organic silt horizon were layers in the 0.75-5.25-inch horizon indicating recent sedimentation, 2) large quantity of decaying leaves and stems in the two upper horizons, 3) gravel and cobbles at 5.25-32 inches, 4) shallowness of the roots, working depth at only 18 inches, maximum 26 inches, 5) reaction pH 7.0 to 7.6, 6) no effervescence above 5.25 inches, moderate to strong on surfaces of pebbles and sand particles below 5.25 inches.

STAND 82 DRYAS OCTOPETALA-KOBRESIA MYOSUROIDES-HEDYSARUM ALPINUM AMERICANUM

This community was found on mountain slopes in the vicinity of Polychrome Pass and he Toglat River in Mt. McKinley National Park. Areas occupied by it are distinctive because of the rich green, carpet-like appearance. According to Murie (1949) mountain sheep prefer this community for winter grazing. The stand studied in detail on August 22, 1949, was on a steep (15°-25°) slope, facing west, along the Toglat River, at an elevation of about 3200 feet. The cover was moderate, 1189 hits. *Dryas octopetala,* 2 to 3 inches tall, made up about 11% of the cover; the sedge, *Kobresia myosuroides* 10%, and Hedysarum next. The resemblance of *K. myosuroides* life-form to that of *Carex filifolia,* of the northern Great Plains is striking. The total number, 31, of species was high, and 26 were hit. The following species had high frequencies but the cover was low; *Carex scirpoidea,* 4 to 7 inches tall, *Salix arctica, S. reticulata,* and *Equisetum arvense.* The inflorescences of *Festuca rubra* and *F. altaica* were 12 to 18 inches high. Shells of the snail, *Succinea strigota* Pfeiffer, determined by Mr. Henry Van Der Schalie, were found on the surface and in the soil. Pellets of manure of mountain sheep were also scattered over the surface. This community is very similar to Nordhagen's (1943) *Kobresietum myosuroides* Association in the *Kobresieto-Dryadion* Alliance in the Order comprising rock communities in mountainous regions.

Important features of the soil profile were 1) the thickness of the dark sandy loam, to 25 inches, then sandy silt to 35.5 inches, and clay with gravel fragments at 35.5-38 inches, 2) apparently a former surface at 18 inches, 3) good distribution of roots to 25 inches, working depth at 26 inches, maximum 37.5 inches, 4) snail shells found on the surface and to a depth of 35.5 inches, 5) ground was frozen at 38 inches, 6) strong to moderate effervescence in most of the profile, none at 35.5-38 inches, strong in the underlying rock, 7) reaction alkaline throughout, pH 7.2-7.8, 8) hummocky surface, 12-15-inch high hummocks, litter and moss 0.5-1 inch thick.

STAND 66 DRYAS ALASKENSIS-D. OCTOPETALA-CAREX MISANDRA-C. BIGELOWII

This community covered much of the area on slopes of Eagle Summit on the Steese Highway, between Fairbanks and Circle. The stand, studied on August 6, 1949, was on a westerly slope of 5° to 10°, at an elevation of about 3880 feet. The plant cover was rather thin, 709 hits, consisting of approximately equal proportions of the 4 species named in the heading which made up 76% of the total cover. The number of vascular species was large, totalling 38, of which 30 were hit (Table 9). The leaves of *Dryas* spp. were usually 3 to 5 inches high. Some of the sedge inflorescences, *Papaver macounii,* and *Polygonum viviparum* reached heights of 8 to 15 inches. The vegetation was an interesting mixture of *Dryas* spp., sedges, dwarf heath shrubs, forbs, mosses and scattered lichens. This area has been grazed by caribou.

Important features of the soil profile were 1) the 5-inch thick peat layer beneath the organic layer at 0-0.75 inch and underlaid to 9.5 inches by clay loam, with rocks in both, 2) silt with gravel and rocks at 9.5-24 inches, and silty gravel with rocks at 24-36.5 inches, 3) excellent drainage to 35 inches where seepage occurred, 4) fairly deep penetration of the roots, working depth at 20.5 inches, maximum about 35 inches, most of the larger roots above 10.5 inches, 5) soil reaction pH 4.6-5.8, 6) no frozen ground to 36.5 inches, as deep as dug.

DRYAS INTEGRIFOLIA-LICHEN COMMUNITIES ON RAISED BEACHES IN VICINITY OF KOTZEBUE

Raised beaches, 2 to 3 or more rods wide, alternated with marsh vegetation on the spit on which Kotzebue is situated. These beaches are low, and gravel is usually within 2 to 4 inches of the surface, often on the surface. Several of these beaches were studied in August, 1949, and in July, 1950. Chief species making up the cover were *Dryas integrifolia, Saxifraga tricuspidata, Empetrum nigrum, Arctostaphylos alpina,* and *Salix reticulata.* Other vascular species were; *Vaccinium uliginosum, V. vitisidea, Ledum decumbens, Betula nana exilis, Salix* spp., *Epilobium latifolium, Pedicularis lanata, Hierochloa alpina, Poa* sp., *Carex* spp. Lichens and mosses cover much of the ground between the vascular plants. The lichens were usually 0.5 to 1 inch high, but in places protected from the wind such as slight depressions and under dwarf shrubs they reached 2 to 2.5 inches in height. Some of the chief species were *Cladonia sylvatica, Cetraria cucullata, C. nivalis, Cornicularia divergens,* and *Thamnolia vermicularis.* Other species were *Cladonia pleurota, C. gracilis* v. *elongata, C. cornuta* v. *cylindrica, C. uncialis, Cetraria islandica*

especially in lower protected spots, *Alectoria ochroleuca, A. nigrescens, Lobaria linita, Peltigera canina, Sphaerophorus globosus,* and *Stereocaulon tomentosum.*

A soil profile in a stand of this kind (Stand 74) is described in the section on Sequence on the Lowlands in the Vicinity of Kotzebue.

DRYAS OCTOPETALA-LICHEN ALPINE COMMUNITIES

Dryas octopetala-lichen communities give a characteristic pale grayish green or gray color to rocky areas above the taller, greener herbaceous vegetation, the green willow communities, or the dark bluish green alders on hills and mountains in many parts of Alaska.

The Dryas-lichen communities are conspicuous from a distance or from the air. The color is due to the old dead leaves which remain attached to the stems, and also to the lichens, to the grayish green living Dryas leaves, and to the numerous species of low herbaceous and shrubby plants. Some of the most characteristic species on a shaly hill about 5 miles northeast of Nome, elevation about 650 feet, on July 8, 1950, were *Diapensia lapponica, Loiseleuria procumbens, Phlox sibirica,* and *Silene acaulis.* Many other species were present in this stand, usually in moderate to low abundance; such as, *Salix reticulata, S. phlebophylla, S. rotundifolia, Cassiope tetragona* in draws especially, *Festuca altaica* in moist protected spots, *Carex montanensis, Pedicularis capitata, P. lanata, Hierochloa alpina, Ledum decumbens, Empetrum nigrum, Polygonum bistorta plumosum Rhododendron kamtschaticum, R. lapponicum, Toffieldia coccinea, T. pusilla, Arenaria rossii, A. arctica, Arnica loiseana, Thalictrum alpinum, Primula egalikensis, Minuartia macrocarpa, Cerastium beeringianum, Lagotis stelleri, Luzula arcuata, Armeria maritima, Saxifraga flagillaris, S. oppositifolia, Androsace chamaejasme, Anemone drummondii, Woodsia glabella, Pinguicula vulgaris, Cardamine purpurea, Astragalus umbellatus Antennaria alaskana, Parrya nudicaulis, Oxytropis nigrescens, Papaver macounii, Hedysarum alpinum americanum, Campanula uniflora, Potentilla vahliana,* and *Zygadenus elegans.* Fourteen species of lichens were collected in this community; *Cladonia rangiferina, C. sylvatica, Cetraria islandica, C. nivalis, C. cucullata, C. juniperina, C. lacunosa, Alectoria ochroleuca, Cornicularia divergens, Dactylina arctica, Ochrolechia frigida, Parmelia omphalodes, Sphaerophorus globosus,* and *Thamnolia vermicularis.*

DISCUSSION OF DRYAS COMMUNITIES

These communities show resemblance to Du Rietz's (1925a) *Dryas octopetala-Cetraria nivalis* Association in southern Norway. They are usually on substrata where the gravel is on or close to the surface and show a dominance of one or more species of *Dryas,* as *D. integrifolia, D. octopetala,* or *D. alaskensis.* One or more codominants, such as *Hedysarum alpinum americanum, Festuca rubra, Kobresia myosuroides, Carex misandra,* and *C. bigelowii* are also present. Species common to several stands are *Carex scirpoidea, Polygonum viviparum,* and *Salix reticulata.* Lichens are often well represented by a variety of species and in abundance, but the growth is usually short. Silt is sparse in the substratum and organic matter is usually limited to horizons near the surface. The root systems vary considerably, depending upon the nature of the substratum, working depths varying from 16 to 23 inches, maximum 17 to 37.5 inches.

DWARF HEATH-LICHEN COMMUNITIES

Dwarf heath-lichen communities are of wide occurrence on more or less gravelly and stony land in the mountains of central Alaska and on hillsides and mountain slopes of northwestern Alaska, and most likely in other parts which were not visited. They are characterized by the abundance of several species of lichens, dwarf heath plants, and other dwarf shrubs. such as *Betula* spp. and *Salix* spp., and scattered herbaceous plants. There is considerable resemblance to the Dryas-lichen communities, but Dryas is usually not abundant in the dwarf heath-lichen communities. There is also similarity in species composition to the scrub birch communities, and in fact, it appears that as the soil becomes finer or as the soil moisture content becomes greater the scrub birch may replace the dwarf heath-lichen, especially at lower elevations. Or the opposite may probably occur if the soil moisture becomes reduced greatly in the scrub birch soil. Stands of the dwarf heath-lichen communities can be recognized readily from the air by the pale greenish gray or pale yellowish gray color, and the velvety appearance. This group of communities corresponds to Nordhagen's (1943) *Loiseleurieto-Arctostaphylion* Alliance in which *Loiseleuria procumbens, Arctostaphylos alpina,* and *Diapensia lapponica* are the chief "characteristic" (Braun-Blanquet's usage, 1932) species. This alliance and the *Phyllodoco-Myrtillion* Alliance (*Phyllodoce coerula, Vaccinium myrtillus*) belong to the dwarf heath shrub order on lime-poor soil. Nordhagen considers the communities (sociations and associations) in this order as very important kinds of vegetation in Norway, because the abundance of lichens furnishes the chief source of food during the winter for tame and wild reindeer. In Norway these communities may occur under trees or shrubs, as well as in the open. Similar communities have been described by Antevs (1932) in the alpine zone of the Mt. Washington Range in New Hampshire, by Trapnell (1933) in Greenland, by Du Rietz (1925a) in southern Norway.

A stand, studied on June 28, 1950, was located at an elevation of about 150 feet above sea-level, on a north-facing slope of about 5°, 10 miles northeast of Nome, on the west side of the Nome River. This community was fairly common in this vicinity, usually surrounded by scrub birch, willow, or sedge communities. The dwarf shrubs and herbaceous plants were scattered and ranged from a few inches to about a foot high (Fig. 32). Occasionally a birch reached a height of 2 or 3 feet. Lichens covered most of

the ground and were usually 1 to 2 inches high, in protected spots as under shrubs and in depressions, 3 to 4 inches high. In 1922 when Palmer (1945, p. 33) conducted his reindeer-range studies on the Dexter Creek "lichen-browse type," 2 miles to the south, the average height of the lichens was 4 inches. The Dexter Creek site was examined, one of Palmer's fenced plots found, and the community was very similar to this. This stand corresponds closely to Nordhagen's (1943) *Betula nana-Empetrum hermaphroditum-Cetraria nivalis* Sociation, in the first alliance named above. According to Norhagen this sociation is widespread in Scandinavia.

The chief vascular species in this stand were; *Betula nana exilis*, usually trailing and up to 1 foot high, rarely 2 to 3 feet high, *Salix pulchra* 6 to 24 inches, *Salix glauca* v. *acutifolia* similar in height, *Vaccinium uliginosum* 3 to 12 inches, *V. vitisidea* 1 to 3 inches, *Loiseleuria procumbens* less than 1 inch, *Empetrum nigrum* 1 to 2 inches, *Lycopodium annotinum* abundant in spots, up to 2.5 inches high, *Carex montanensis* 2 to 4 inches above the lichens, *Arctostaphylos alpina* creeping stems up to 2 to 3 inches high, *Ledum decumbens* 1 to 6 inches, *Festuca altaica, Luzula multiflora, Hierochloe alpina, Spiraea beauverdiana, Dryas octopetala, Salix reticulata, Anemone narcissiflora, Parrya nudicaulis, Pedicularis* sp., *Polygonum bistorta* ssp. *plumosum, Cassiope stellariana, Dodecatheon frigidum, Potentilla fruticosa*, and *Caltha palustris*.

The most common and abundant lichens were *Cladonia sylvatica, C. rangiferina, Cetraria cucullata, Cladonia verticillata, C. cornuta cylindrica, Stereocaulon tomentosum* especially in bare spots, and *Cladonia gonecha*. Moderately numerous to scarce were *Ochrolechia frigida, Pertusaria coccodes, Cladonia delessertii, Pilophorus cereolus, Thamnolia vermicularis, Nephroma arcticum, Cladonia pleurota*, and *C. macilenta* v. *squamigera*. Common mosses were *Polytrichum piliferum, Hylocomium splendens, Drepanocladus uncinatus, Bryum* sp., *Ptilidium ciliare*, and the little clubmoss, *Selaginella selaginoides*.

Detailed description of the soil profile:

The surface was covered with moss and lichens, the former up to 2 inches thick, often lichens were found invading and growing on the moss.

0-1.75 inch. Dark brown, organic loam, very few fine rock flakes, moist, loose, and soft, roots very numerous, pH 4.6.

1.75-5.25 inches. Dark reddish brown, silt loam with much decayed organic matter, much more compact than horizon above, picks out in small blocks 1 inch through, some gravel and flat rock particles of highly metamorphic mica-schist interspersed, moist, roots scattered, pH 4.8.

5.25-14 inches. Loose, crumbly schist rock, mostly thin pieces rarely over an inch long, roots scarce to 14 inches, wet, pH 4.8.

A stand near the Dahl Creek Air Strip, between Shungnak and Kobuk on the Kobuk River, about 160 miles due east of Kotzebue, was examined on August 13, 1949. Low shrubs, 12 to 18 inches high, including *Vaccinium uliginosum* with numerous ripe berries, *Ledum decumbens*, and *Betula exilis nana*, were scattered over the gently sloping outwash plain below the mouth of a canyon. *Vaccinium vitisidea* occurred generally, and small white spruce saplings were scattered. Lichens formed a dense growth over the ground, usually to a height of 1 to 2 inches, but under shrubs they were often 3 to 4 inches high. The chief species were *Cladonia mitis, C. gracilis, C. rangiferina, C. pleurota, C. uncialis, C. furcata, C. amaurocraea, C. sylvatica, Cetraria nivalis, C. cucullata, C. islandica, Stereocaulon* sp., and *Lobaria varrucosa* (prob.). The soil varied from silt with much sand to gravel and rock. In some spots, more exposed to the wind, the ground was bare and eroding.

LUETKIA PECTINATA ALPINE COMMUNITIES

Two very interesting communities were found on opposite sides of hummocks at an elevation of about 4000 feet in the Talkeetna Mountains, near the Independence Mine, north of Palmer, on July 26-27, 1949. The general slope of about 10° was toward the west and southwest. Rocks covered with vegetation were scattered over the area, and large snow drifts were thawing in depressions. The hummocks were 6 to 12 inches high. The gray color of the south-facing, down hill sides were in striking contrast to the north-facing, upslope sides. The difference in color was due largely to the greater abundance of lichens and the lesser abundance of vascular species on the south sides. As shown in Table 9 the species composition of these stands is distinctive as compared to other stands. Species that were more abundant on the north sides of the hummocks were *Cassiope stellerianum, Lycopodium* spp., and *Luetkia pectinata*. The mosses did not differ much in abundance on the two sides. The soil profile showed differences on the two sides; on the north side was a leached horizon, the root systems penetrated somewhat deeper, and there was more and deeper dark soil than on the south side. These stands show some resemblance to the small isolated stands at about 5000 feet on Mt. Bertha in the Fairweather Range in the Glacier Bay National Monument, described by Cooper (1942). He pointed out the resemblance of the Mt. Bertha stands to the alpine mat of southeastern Alaska.

STAND 53 LUETKIA PECTINATA-CASSIOPE STELLERIANUM-LYCOPODIUM ALPINUM

There were 12 vascular species, 6 kinds of lichens, and a moss species on the north sides of the hummocks (Table 9). The species listed above made up 80% of the cover of 506 points. This stand resembles somewhat Nordhagen's (1943) *Cassiopetum hypnoides* Association in the order comprising snow-field communities and Gjaerevoll's (1949) *Cassiope hypnoides* sociation in "snow-bed vegetation" of Oviksfjällen Mountains, Jämtland, Sweden. The dense mat of plants was about an inch high, with flower stalks of Cassiope, blooming, 2.5 inches high, and grass blades 3.5 inches high. The lower part of this layer was largely decaying plant debris.

Important features of the soil profile were 1) the dense carpet of vegetation, 2) leached layer at 0.5-2 inches, 3) silt to 15 inches, silty gravel below that, and colored brown to depth of 19.75 inches, 4) softness of the 8.5-15-inch layer, 5) no effervescence, 6) reaction acid, pH 4.8-5.4, 7) working depth of roots at 17.5 inches, maximum 24 inches.

STAND 54 LUETKIA PECTINATA-CLADONIA SPP.-LYCOPODIUM ALPINUM

This stand, on the south sides of hummocks, had 9 vascular species, 9 kinds of lichens, and 2 kinds of mosses (Table 9). The cover index was low, 386 hits, 46% of which was lichens, and about 40% of *Luetkia* and *Lycopodium*. The carpet of vegetation was about 0.5 inch thick, some of the lichens extending 1.5 to 2 inches higher.

Important features of the soil profile were 1) fairly dense layer of mostly lichens, 2) dense layer of stems and roots at 0-0.75 inch, 3) dark brown silt loam at 0.75-6.75 inches, not present on the north side, 4) reddish brown silt at 6.75-8.75 inches, not present on the north side, with sandy silt and gravel below, 5) much greater and deeper development of dark soil than on the north side, 6) working depth of roots at 15 inches, maximum 22 inches, 7) reaction pH 5.0-5.2.

SUMMARY

1. A large number of plant communities occurring in various parts of western Alaska, from Kodiak Island in the southwest to Kotzebue in the northwest and Big Delta in the northeast were investigated in this study. These communities included coastal strand and salt marsh vegetation, several kinds of grassland, upland marshes and bogs, forest and shrub, dwarf shrub-lichen, Dryas, and Luetkia communities. A classified list is given in the Table of Contents. Some of the communities, especially in hummocky marsh areas and in the tundra are complexes, or mosaics of micro-communities.

2. The vegetation in representative stands was analyzed according to kinds of species, cover, frequency, and some data were secured on miscellaneous characteristics such as height growth, phenology, and succession. Soil profiles were described in most of the stands. Thorough knowledge of communities, including soil characteristics, is essential to the sound use and development of these basic plant resources, especially in Alaska where much of the land is not suitable for cultivation.

3. The close similarity of many of the communities to those in other regions, especially in Norway, is pointed out.

4. The sequence of communities on sandy seashores and estuaries, beginning near high-tide line and proceeding to meadows includes 1) *Arenaria peploides-Mertensia maritima* community-fragments; 2) *Elymus mollis*, or *E. mollis-Lathyrus maritimus* (in places *Poa eminens*) communities on sand dunes and sandy ridges; 3) mixed grass-forb communities comprising as dominants one or more of the following species: *Elymus mollis, Festuca rubra, F. altaica, Calamagrostis canadensis*, and prominent forbs such as, *Achillea borealis* and *Lupinus nootkatensis;* and 4) meadows in which the dominants are one or more of the following species: *Agropyron trachycaulum, Festuca rubra, Calamagrostis canadensis, Poa palustris*, with a variety of forbs such as *Achillea borealis, Lathyrus palustris, Hedysarum alpinum americanum, Dodecatheon macrocarpum*, and *Smilacina stellata.* Willows occur as early woody invaders. The soil profiles vary from mostly sand or gravel, almost devoid of organic matter in the first group, to deep, well developed soil with much organic matter in the last. Many of the dunes on estuaries on Kodiak Island consist of ash which erodes easily when the protective cover of Elymus is broken. The root systems in these communities are usually well developed and penetrate deeply.

5. The sequence of communities on silty estuaries and coasts, beginning on silty shores subject to daily submersion by saline or brackish water begins with early invaders as *Puccinellia phryganodes, Salicornea herbacea*, and *Suaeda maritima*, in community fragments or as individuals, and culminates in meadow communities. Willows and alders, followed by cottonwood forest, replace the herbaceous communities in many places. The soils in these communities are usually compact silt and peat, often showing stratification, usually with poor internal drainage, and are only slightly developed. On Kodiak Island the 1912 ash layers, primary and secondary deposits, were up to about 2 feet thick, and a layer, usually 1 to 2.5 inches thick, of mostly organic material had formed on top of the ash. The surface drainage was especially poor in communities of *Carex cryptocarpa* and *Calamagrostis canadensis-Myrica gale.* The root systems were comparatively shallow, maximum depths less than 30 inches, the penetration limited in places by the shallow level of standing water, in others by the composition of the peat, etc.

6. Communities examined on the lowlands in the vicinity of Kotzebue were 1) the *Carex subspathacea* community on wet peat in shallow brackish water or subject to overflow with such water; 2) the *Carex rariflora* community on peaty material and silt, less subject to overflow with brackish water; 3) the *Carex aquatilis-C. rotundata* in shallow basins not subject to overflow with brackish water; 4) the *Ledum decumbens-Vaccinium vitisidea-Cetraria* spp. community on mounds and ridges; and 5) the *Dryas integrifolia*-Lichens community on low, gravelly, raised beaches. The depth to the frozen ground varied considerably, from below 3 feet in the first community, 15 inches or less in the second, about 22 inches in the third, about 10.5 inches in the fourth depending upon the thickness of the plant cover, to below 28 inches in the fifth. Frost action was an important factor in most of these communities, in addition to others such as soil moisture, depth to permafrost, nature of the substratum, and exposure to drying winter winds. The root systems were shal-

low, maximum depths ranging from 10.5 to 22 inches in the various communities.

7. The grassland communities on the uplands were divided into 5 groups: 1) Cliff Meadows, 2) Tall Grass-Forb with *Calamagrostis canadensis* as the Chief Dominant, 3) Medium Tall Grass-Forb with *Festuca altaica* as the Chief Dominant, 4) *Agropyron trachycaulum* communities, and 5) Miscellaneous Upland Grassland communities. The Cliff Meadow communities, near the edges of cliffs along the coasts of Kodiak Island were especially well developed, containing 47 and 36 species in the two stands that were studied. The dominant species were *Deschampsia beringensis, Poa glauca, Carex macrochaeta, Calamagrostis canadensis,* and some forbs. Some of the chief forbs in the second group were *Epilobium angustifolium, Heracleum lanatum, Angelica* spp., *Geranium erianthum, Sanguisorba sitchensis,* and several tall ferns. Floristically the third group is similar to the second group, except that *Festuca altaica* is the chief dominant. Many forb species were common to both groups. The fourth group, located in the Matanuska Valley, were fairly open, located on steep south-facing slopes with fairly well developed, deep, porous soil. Associated forbs were similar to those in the two preceding groups. The fifth group comprised 5 stands on steep, south-facing slopes in interior Alaska, with *Calamagrostis purpurescens, Poa glauca, Elymus innovatus,* and *Artemisia frigida* as the chief dominants. The sixth stand was a mountain meadow along the Delta River, in which *Festuca rubra, Carex supina,* and *Agropyron latiglume* were the dominants.

8. Shrub and Forest communities that were studied, included alder, scrub birch, willow, Sitka spruce, white spruce, and Alaska birch stands.

9. Upland Marsh and Meadow communities, 8 of which were studied, are characterized by species common to many of them, such as *Eriophorum angustifolium, Salix reticulata, S. pulchra, Carex bigelowii, Polygonum viviparum,* and mosses. The cover was usually good, the number of species high, the saturated substratum usually composed of peat and silt, frost action and solifluction important soil factors, and the root systems shallow.

10. Two stands in the Upland Bogs group were studied. They were characterized by the abundance of Sphagnum, dwarf shrubs including *Betula nana exilis, Vaccinium uliginosum, V. vitisidea, V. oxycoccus, Rubus chamaemorus, Salix pulchra, Andromeda polifolia, Myrica gale, Ledum decumbens, Potentilla palustris;* by sedges, especially *Carex bigelowii;* and by invasion in places by *Picea mariana.*

11. Dryas Communities, widespread on gravelly substratum in Alpine and Arctic regions, are characterized by the dominance of one or more species of *Dryas,* and one or more codominants such as *Hedysarum alpinum americanum, Festuca rubra, Kobresia myosuroides, Carex misandra,* and *C. bigelowii.* Species common to several stands were *Carex scirpoidea, Polygonum viviparum,* and *Salix reticulata.* Lichens formed a dense and thick layer in some of the stands. These communities are important in pioneering on gravelly sites.

12. Dwarf Heath-Lichen Commmunities are of wide occurrence on gravelly and stony land in mountains of central Alaska and on hillsides and mountain slopes in northwestern Alaska. They are characterized by the abundance of lichens, particularly species of *Cladonia* and *Cetraria,* by dwarf shrubs such as *Betula* spp., *Salix* spp., *Vaccinium* spp., *Loiseleuria procumbens, Empetrum nigrum,* and by such herbaceous species as *Carex montanensis, Luzula multiflora, Hierochloe alpina,* and *Pedicularis* sp. These communities are of great economic importance because the abundance of lichens furnishes much winter feed for reindeer and caribou.

13. The *Luetkia pectinata* Alpine Communities were studied in one location, the Talkeetna Mountains. The chief species in addition to *Luetkia* were *Lycopodium alpinum, Cassiope stellerianum;* especially on the north sides of hummocks; and *Cladonia* spp. on the south sides. The working depths of the roots were at 15-17.5 inches, maximum depths 22-24 inches.

14. Several species were of wide occurrence in many kinds of communities (see Appendix). Species showing such wide distribution, due probably, to their wide ecological amplitude, were: *Calamagrostis canadensis, Festuca rubra, F. altaica, Poa glauca, Trisetum spicatum, Luzula multiflora, L. parviflora, Epilobium angustifolium, Equisetum arvense, Achillea borealis, Trientalis europea arctica, Anemone narcissiflora, Galium boreale, Iris setosa, Lupinus nootkatensis, Parnassia palustris, Pedicularis capitata, Petasites frigidus, Polemonium acutiflorum, Polygonum viviparum, Potentilla pacifica, Sanguisorba sitchensis, Sedum roseum, Solidago multiradiata, Vaccinium uliginosum, V. vitisidea, Betula nana exilis, Empetrum nigrum, Potentilla fruticosa, Rosa acicularis, Rubus stellatus, Salix fuscescens, S. glauca, S. pulchra, S. reticulata, Spiraea beauverdiana, Hylocomium splendens,* and *Pleurozium schreberi.*

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APPENDIX A

Check List of Species Tabulated According to Classes of Communities. 1-Sandy and Gravelly Strand, 2-Silty Estuaries and Coasts, 3-Lowland Meadows, 4-Kotzebue Lowlands, 5-Cliff Meadow, 6-Tall Grass-Forbs with *Calamagrostis canadensis* as the Major Dominant, 7-Medium Tall Grass-Forbs with *Festuca altaica* as the Major Dominant, 8-*Agropyron trachycaulum*, 9-Miscellaneous Upland, 10-Shrub and Forest, 11-Upland Marsh and Meadow, 12-Upland Bog, 13-Dryas, 14-Scrub Birch, 15-Dwarf Shrub-Lichen, 16-Luetkia Alpine.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
GRASSES																
Agropyron latiglume (Scribn. & Sm.) Rydb.									x							
A. spicatum (Pursh) Scribn.									x							
A. trachycaulum (Link) Hitchc.			x					x								
Agrostis scabra Willd.						x										
Agrostis sp.			x					x	x							
Arctagrostis arundinacea (Trin.) Beal.													x			
A. latifolia (R. Br.) Griseb.							x				x		x			
Bromus pumpellianus Scribn.									x							
Bromus sp.						x										
Calamagrostis canadensis (Michx.) Beauv.	x	x	x		x	x	x			x	x	x				
C. deschampsioides Trin.		x		x												
C. inexpansa A. Gray			x													
C. neglecta (Ehrh.) Gaertn.											x					
C. purpurescens R. Br.									x				x			
Calamagrostis sp.							x									
Danthonia intermedia Vasey							x									
Deschampsia atropurpurea (Wahl.) Scheele							x									
D. beringensis Hult.	x	x	x		x	x				x						
D. caespitosa (L.) Beauv.				x												
Deschampsia sp.											x					
Dupontia fisheri R. Br.				x												
Elymus innovatus Beal							x		x							
E. macounii Vasey								x								
E. mollis Trin.	x	x	x	x	x	x										
Festuca altaica Trin.	x		x			x	x				x	x		x		
F. brachyphylla Schult.													x			
F. rubra L.	x	x	x	x	x	x	x		x				x			
Festuca sp.						x										
Hierochloe alpina (SW.) Roem. & Schult.							x						x		x	
H. odorata (L.) Beauv.	x	x	x		x	x										
Hordeum brachyantherum Nevski	x	x	x			x										
H. jubatum L.						x										
Phleum alpinum L.		x			x	x	x									
P. pratense L.			x			x										
Poa alpina L.									x				x			
P. arctica R. Br.						x	x				x	x	x			
P. compressa L.						x										
P. eminens Presl.	x	x	x	x												
P. glauca Vahl					x	x	x		x							
P. hispidula Vasey	x															
P. palustris L.			x			x										
P. paucispicula Scribn.							x									
P. pratensis L.			x						x							
Poa sp.		x			x	x	x	x		x	x		x			x
Puccinellia borealis Swallen				x												
P. glabra Swallen		x														
P. phryganodes (Trin.) Scribn. & Merr.		x														
P. triflora Swallen		x														
Trisetum spicatum (L) Richt	x		x		x						x		x			
SEDGES AND RUSHES																
Carex anthoxanthea Presl.							x				x					
C. aquatilis Wahl.				x						x	x	x				
C. atrofusca Schk.				x												
C. bicolor All.				x												
C. bigelowii Torr.				x			x				x	x	x	x		
C. bipartata All.							x				x					
C. brunnescens (Pers.) Poir						x	x			x						
C. canescens L.		x														
C. capillaris L.				x									x			
C. capitata L.													x			
C. cryptocarpa C. A. Mey.	x	x	x													
C. glareosa Wahl.		x	x	x												
C. gmelini Hook. & Arn.	x		x													
C. hindsii C. B. Clarke			x													
C. livida (Wahl.) Willd.				x												
C. lugens Holm										x						
C. mackenziei Kretch.		x														
C. macloviana d'Urv. *pachystachya* (Cham.) Hult.		x				x										
C. macrochaeta C. A Mey.					x	x	x			x						
C. meadii Dewey													x			
C. membranacea Hook.											x		x			
C. mertensii Prescott						x										
C. misandra R. Br.													x			
C. montanensis Bailey							x						x		x	
C. nesophila Holm				x						x						
C. obtusata Lilj.							x									
C. physocarpa Presl.				x							x					

APPENDIX A—Continued

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
C. pluriflora Hult.		x									x					
C. podocarpa R. Br.							x									
C. praticola Rydb.							x									
C. ramenskii Komarov		x														
C. rariflora (Wahl.) J. F. Smith				x												
C. rotundata Wahl.				x							x					
C. rupestris All.													x			
C. scirpoidea Michx.													x			
C. spectabilis Dewey							x				x					
C. subspathacea Wormskj.				x												
C. supina Willd. *spaniocarpa* (Steud.) Hult.									x							
C. tenuiflora Wahl.											x					
C. vaginata Tausch.										x	x		x			
Carex sp.	x	x	x	x		x	x		x				x			x
Eleocharis kamtschatica (C. A. Mey.) Kom.		x														
E. macrostachya Brit.											x					
Eriophorum angustifolium Roth.				x							x					
E. chamissonis C. A. Mey.				x												
E. scheuchzeri Hoppe s. lat.		x														
E. vaginatum L.											x					
Juncus albescens (Lge.) Fern.											x					
J. arcticus Willd.													x			
J. balticus Willd.		x														
J. filiformis L.		x														
Kobresia myosuroides (Vill.) Fiori & Paol.													x			
Luzula arcuata Wahl.													x			
L. confusa Lindeb.													x			
L. multiflora (Retz.) Lej.	x	x	x		x	x	x		x	x	x		x		x	
L. parviflora (Ehrh.) Desv.							x									
L. rufescens Fisch.							x									
Luzula sp.							x						x			x
Scirpus caespitosus L. *callosus* Bigel.				x							x					
S. pacificus Brill.		x														
FORBS.																
Achillea borealis Bongard	x	x	x		x	x	x	x	x	x						
Aconitum delphinifolium DC.					x	x	x			x	x					
Actaea spicata L.						x										
Androsace chamaejasme Host. *lehmanniana* (Spreng.) Hult.				x									x			
A. septentrionalis L.									x							
Anemone drummondii Wats.													x			
A. multifida Poir.									x							
A. narcissiflora L.					x		x			x					x	
A. parviflora Michx.							x				x		x			
A. patens L. *multifida* (Pritzel) Zamess.									x							
A. richardsonii Hook.							x				x					
Angelica genuflexa Nutt.						x										
A. lucida L.	x	x	x		x	x	x									
Antennaria alaskana Malte													x			
A. isolepis Greene							x									
A. monocephala DC.							x									
A. nitida Greene								x								
A. oxyphylla Greene									x							
A. pallida E. Nels.								x								
Antennaria sp.									x							
Aquilegia formosa Fisch.						x										
Arabis divaricarpa A. Nels.									x							
A. hirsuta (L.) Scop.			x													
A. holboelli Hornem.									x							
A. lyrata L. *kamchatica* (Fisch.) Hult.						x										
Arenaria arctica Stev.													x			
A. laricifolia (L.) Gray									x							
A. lateriflora L.			x		x	x	x	x	x	x						
A. peploides L.	x															
A. rossii R. Br.													x			
Armeria maritima (Mill.) Willd. *purpurea* (M. & K.) Lawr.													x			
Arnica loiseana frigida (Meyers) Maguire													x			
Arnica sp.					x	x										
Artemisia arctica Less.						x	x			x	x					
A. dracunculoides Pursh									x							
A. frigida Willd.									x							
A. tilesii Ledeb.						x	x									
Aster junceus Ait.			x													
A. junciformis Rydb.			x													
A. sibiricus L.							x	x	x				x			
Aster sp.											x					
Astragalus alpinus L.									x							
A. umbellatus Bunge							x						x			
Athyrium filix-femina (L.) Roth.		x				x				x						
Atriplex gmelini C. A. Mey.		x														
Botrychium boreale (SW.) Milde.						x	x									
B. lunaria (L.) SW.						x	x	x								
Boykinia richardsonii (Hook.) Gray							x				x					
Bupleurom americanum Coult. & Rose									x							
Caltha leptosepala DC.											x					
C. palustris L.															x	
Campanula lasiocarpa Cham.							x									
C. rotundifolia L.					x	x										
C. uniflora L.													x			
Cardamine pratensis L.														x		
C. purpurea C. & S.											x		x			

APPENDIX A—Continued

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
C. umbellata Greene	x					x										
Castilleja pallida (L.) Kunth						x		x								
C. unalaschkensis (C. & S.) Malte			x		x	x	x									
Castilleja sp.				x												
Cerastium beeringianum C. & S.							x		x				x	x		
Chrysanthemum arcticum L.		x		x												
Cicuta douglasii (DC.) Coult. & Rose		x				x				x						
C. mackenzieana Raup		x														
Cicuta sp.			x													
Claytonia sarmentosa C. A. Mey.							x				x			x		x
C. sibirica L.						x										
Claytonia sp.							x				x					
Cochlearia officinalis L.	x	x														
Conioselinum benthami (Wats.) Fern.			x		x	x										
Corallorrhiza trifida Chatelin										x						
Cornus canadensis L.						x	x			x				x		
C. canadensis intermedia Farr.							x									
C. suecica L.	x									x						
Corydalis pauciflora (Steph.) Pres.						x				x						
Cypripedium guttatum Swartz					x											
Delphinium glaucum Wats.										x						
Dodecatheon frigidum C. & S.							x			x	x			x	x	
D. macrocarpum (Gray) Knuth	x		x		x	x										
Draba aurea Vahl									x							
D. glabella Pursh						x			x							
D. lanceolata Royle									x							
Drosera rotundifolia L.												x				
Dryopteris austriaca (Jacq.) Woynar						x				x						
D. disjuncta (Ledeb.) Morton					x	x	x			x						
D. oreopteris (E.) Maxon						x	x									
D. phegopteris (L) C. Chr.						x										
Epilobium alpinum L.							x									
E. angustifolium L.	x	x	x		x	x	x	x	x	x		x	x	x		
E. latifolium L.							x						x			
Epilobium sp.		x														
Equisetum alaskanum Eaton							x				x					
E. arvense L.	x	x	x		x	x	x		x	x	x		x			
E. fluviatile L.		x										x				
E. palustre L.											x	x				
E. pratense Ehrh.						x	x	x	x	x						
E. scirpoides Michx.					x		x									
E. sylvaticum L.						x				x						
E. variegatum Schleich.											x		x			
Equisetum sp.		x			x	x										
Erigeron acris L. *asteroides* (Andrz.) DC.								x								
E. peregrinus (Pursh) Greene							x				x					
Erigeron sp.									x							
Eritrichium aretioides (C. & S.) DC.													x			
Erysimum inconspicuum (Wats.) MacM.									x							
Eutrema edwardsii R. Br.													x			
Fragaria sp.						x										
Fritillaria camtchatcensis (L.) Ker.			x		x	x	x									
Galium boreale L.			x		x	x	x		x	x						
G. trifidum L.		x														
G. triflorum Michx.						x										
Gentiana glauca Pall.						x										
G. propinqua Rich.						x	x		x				x			
G. prostrata Haenke													x			
Gentiana sp.			x													
Geranium erianthum DC.					x	x	x			x						
Geum calthifolium Menz.					x	x										
G. macrophyllum Willd.	x	x	x			x		x								
Glaux maritima L.		x														
Hedysarum alpinum L. *americanum* (Michx.) Fedtsch.	x		x										x			
Heracleum lanatum Michx.					x	x				x						
Hippuris vulgaris L.		x									x					
Iris setosa Pall.	x		x		x	x				x		x				
I. setosa Pall. *interior* (E. And.) Hult.											x					
Lacotis stelleri Trautv.													x	x		
Lathyrus maritimus (L.) Bigel.	x	x	x			x										
L. palustris L. *pilosus* (Cham.) Hult.		x	x			x		x								
L. pratensis L.					x											
Ligusticum hulteni Fern.	x	x	x			x										
Limnorchis dilatata (Pursh) Rydb.						x					x					
Linum lewisii Pursh									x							
Listera cordata (L.) R. Br.										x						x
Lomatogonium rotatum (L.) Fries ex Nyman	x			x												
Lupinus nootkatensis Donn.	x	x	x		x	x	x									
L. polophyllus Lindl.							x									
Lychnis dawsonii (B. L. R.) J. P. And.									x							
Lycopodium alpinum L.							x									x
L. annotinum L.						x				x	x				x	
L. clavatum L. *monostachyon* G. & H.							x									
L. selago L.																x
Menyanthes trifoliata L.											x					
Mertensia maritima (L.) S. F. Gray	x															
M. paniculata (Ait.) G. Don.						x	x	x		x						
Minuartia macrocarpa (Pursh) Stenf.													x			
Moneses uniflora (L.) Gray										x						
Montia laprosperma Cham.				x												
Myosotis alpestris F. W. Schmidt							x				x		x			
Orchis aristata Fisch.					x	x										

APPENDIX A—Continued

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Oxytropis gracilis (A. Nels.) K. Schum.									x							
O. nigrescens (Pall.) Fisch. *pygmaea* (Pall.) Hult.													x			
O. scammaniana Hult.													x			
O. viscidula (Rydb.) Tides.									x				x			
Papaver macounii Greene													x	x		
Papaver sp.											x					
Parnassia kotzebuei C. & S.							x									
P. palustris L.	x		x	x	x	x		x			x		x			
Parrya nudicaulis (L.) Regel.													x	x	x*	
Pedicularis arctica R. Br.										x						
P. capitata Adams							x			x	x		x			
P. labradorica Panzer											x	x		x		
P. lanata Willd.													x			
P. langsdorfii Fisch.													x			
P. oederi Vahl														x		
P. pennellii Hult.				x												
P. sudetica Willd.				x			x				x		x			
P. verticillata L.					x		x		x							
Pedicularis sp.															x	
Peramium repens (L.) Sal. *ophinoides* Fern.										x						
Petasites frigidus (L.) Fries						x	x				x	x		x		
P. hyperborea Rydb.						x										
Phlox sibirica L.													x			
Pinguicula vulgaris L.													x			
Plantago canescens Adams									x							
P. juncoides Lam.	x	x														
P. septata Morris									x							
Polemonium pulcherrimum Pors.									x							
P. acutiflorum Willd.	x	x	x			x	x			x	x					
Polygonum alaskanum (Small) Wright						x	x									
P. bistorta L. *plumosum* (Small) Hult.							x				x		x		x	
P. viviparum L.					x		x				x	x	x			
Potentilla arguta Pursh									x							
P. chamissonis Hult.									x							
P. nivea L.									x							
P. pacifica Howell	x	x	x	x												
P. palustris (L.) Scop.		x									x	x				
P. pennsylvanica L.									x							
P. vahliana Lehm.													x			
P. villosa Pall.					x											
P. virgulata A. Nels.								x								
Prenanthes sp.	x				x					x						
Primula egalikensis Wormskj.													x			
P. parvifolia Duby										x						
Primula sp.				x												
Pyrola asarifolia Michx.										x						
P. asarifolia incarnata (DC.) Fern.										x						
P. chlorantha Swartz.										x						
P. grandiflora Radius							x				x					
P. secunda L.										x	x					
P. virens Schweig.										x						
Ranunculus bongardii Greene	x															
R. cymbalaria Pursh		x														
R. lapponicus L.											x					
R. occidentalis Nutt.							x									x
R. pedatifidus Sm.										x						
R. sulphureus Phipps											x					
Ranunculus sp.											x					
Rhinanthus borealis Sternb.	x	x	x		x	x										
Rhinnanthus sp.								x								
Rumex acetosella L.						x										
R. arcticus Trautv.										x						
R. fenestratus Greene		x														
Salicornea herbacea L.		x														
Sanguisorba sitchensis C. A. Mey.		x	x		x	x	x			x	x					
Saussurea angustifolia DC.							x				x		x			
S. subsinuata Ledeb.				x												
Saxifraga bronchialis L. *funstonii* (Small) Hult.							x									
S. flagellaris Willd.													x			
S. hieracifolia W. & K.							x				x			x		
S. lyallii Engler											x					
S. oppositifolia L.													x			
S. punctata L. *nelsoniana* (D. Don.) Hult.							x						x			
S. reflexa Hook.							x		x							
S. tricuspidata Retz.							x		x							
Sedum roseum (L.) Scop.						x	x			x	x					
Selaginella selaginoides (L.) Link														x	x	
S. sibirica (Milde.) Hieron.									x							
Senecio atropurpurea (Ledeb.) Tedtsch.														x		
S. coterminus Greenm.									x							
S. fridigus Less.											x					
S. lugens Richards							x									
S. pauciflorus Pursh								x								
S. pseudo-arnica Less.	x															
S. triangularis Hook.						x	x									
Sibbaldia procumbens L.							x									
Silene acaulis L.													x			
Smilacina stellata (L.) Desf.			x			x			x							
Solidago multiradiata Ait.					x		x	x	x							
Solidago sp.	x	x	x		x	x										

APPENDIX A—Continued

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Spergularia canadensis (Pers.) G. Don		x														
Spiranthes romanzoffiana C. & S.												x				
Stellaria calycantha Bong.						x										
S. crispa C. & S.										x						
S. humifusa Rottb.	x	x		x												
S. laeta Rich.	x						x				x					
S. longifolia Muhl.			x													
S. longipes Goldie							x		x		x		x			
S. sitchana Steud.										x						
Stellaria sp.					x	x										
Streptopus amplexifolius (L.) DC.						x				x						
Suaeda maritima (L.) Dumort		x														
Swertia perennis L.											x					
Taraxacum sp.			x				x	x								
Thalictrum alpinum L.							x				x		x	x		
Tofieldia coccinea Rich.				x									x			
T. pusilla (Michx.) Pres.											x		x			
Trientalis europaea L. *arctica* (Fisch.) Hult.	x	x	x		x	x	x			x	x					
Trifolium pratense L.						x										
T. repens L.						x										
Triglochin maritima L.		x														
T. palustris L.		x									x					
Valeriana capitata Pall.							x			x	x					
V. sitchensis Bong.						x										
Veratrum eschscholtzii A. Gray					x	x	x			x						
Veronica serpyllifolia L.	x															
V. wormskjoldii R. & S.							x									
Viola adunca Smith					x	x	x				x					
V. langsdorfii Fisch.			x		x	x				x						
Viola sp.							x									
Woodsia glabella R. Br.										x			x			
Zygadenus elegans Pursh							x		x				x			
SHRUBS AND TREES																
Alnus fruticosa Rupr.		x				x	x			x						
A. fruticosa sinuata (Regel) Hult.										x						
A. tenuifolia Nutt.												x				
Amelanchier alnifolia Nutt.									x							
Andromeda polifolia L.				x						x	x	x		x		
Arctostaphylos alpina (L.) Spreng.				x	?						x		x		x	
A. rubra (Fern.) Rhed. & Wils.													x			
A. uva-ursi (L.) Spreng.							x									
Betula glandulosa Michx.														x		
B. nana exilis (Sukatch.) Hult.				x			x				x	x		x	x	
B. resinifera Britt.						x		x		x				x		
Cassiope stelleriana (Pall.) DC.															x	x
C. tetragona (L.) D. Don.							x				x		x			
Chamaedaphne calyculata (L.) Moench.												x				
Diapensia lapponica (L.) *obovata* (F. Sch.) Hult.													x			
Dryas alaskensis A. E. Pors.											x		x			
D. integrifolia M. Vahl.											x		x			
D. octopetala L.							x			x	x		x		x	
Empetrum nigrum L.				x		x	x			x	x		x	x	x	x
Juniperus communis L. *montana* Ait.						x										
J. horizontalis Moench.									x							
Ledum decumbens (Ait.) Lodd.				x			x				x	x	x	x	x	
L. groenlandicum Ceder.							x			x						
Linnaea borealis L.							x			x						
Loiseleuria procumbens (L.) Desv.						x	x						x		x	
Luetkia pectinata (Pursh) Kuntze							x									x
Menziesia ferruginea Smith										x						
Myrica gale L.		x										x				
Oplopanax horridus (Sm.) Miq.										x						
Oxycoccus microcarpus Turcz.		x									x	x				
Picea glauca (Moench) Voss							x			x				x		
P. mariana (Mill.) B. S. P.										x		x				
P. sitchensis (Bong.) Carr.					x	x				x						
Populus tacamahacca Mill.							x			x						
P. tremuloides Michx.							x	x		x						
P. tricocarpa Torr. & Gray						x				x						
Potentilla fruticosa L.										x	x	x	x		x	
Rhodendron kamtschaticum Pall.													x			
R. lapponicum (L.) Wahl.													x			
Ribes laxiflorum Pursh						x				x						
R. triste Pall.										x						
Rosa acicularis Lidl.			x			x	x	x	x	x						
Rubus alaskensis Bailey							x									
R. arcticus L.						x										
R. chamaemorus L.				x						x	x	x	x			x
R. pedatus Smith										x						
R. spectabilis Pursh						x				x						
R. stellatus Smith					x	x	x				x		x	x		
R. strigosus Michx.			x			x		x	x							
Rubus sp.						x										
Salix alaxensis (And.) Cov.										x			x			
S. arbusculoides Ands.													x			
S. arctica Pall.											x		x			
S. barclayi Ands.						x	x			x						
S. bebbiana Sargent			x					x		x						
S. fuscescens Andersson		x		x												
S. fuscescens And. *reducta* Ball				x							x	x				
S. glauca L. *acutifolia* (Hook.) Schn.							x							x	x	
S. niphoclada Rydb											x					
S. ovalifolia Trautv.				x												

APPENDIX A—Continued

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
S. phleobophylla Andersson													x			
S. polaris selynensis Raup							x				x					x
S. pulchra Cham.										x	x	x	x	x	x	
S. reticulata L.							x			x	x		x	x	x	
S. richardsonii Hooker				x						x	x	x	x			
S. rotundifolia Trautv.													x			
S. scouleriana Bar.										x						
S. sitchensis Sans.		x				x	x									
Salix sp.					x		x				x	x				
Sambucus racemosa L. *pubens* (Michx.) Hult.						x				x						
Spiraea beauverdiana Schneid.						x	x			x				x	x	
Vaccinium caespitosum Michx.						x	x									
V. ovalifolium Smith										?						
V. uliginosum L.				x		x	x			x	x	x	x	x	x	
V. vitisidea L.				x			x			x	x	x	x	x	x	
Viburnum edule (Michx.) Raf.						x	x			x						
MOSSES																
Aulocomnium palustre (Web. & Mohr.) Schaegr.											x	x				
Bryum sp.										x				x	x	
Camptothecium nitens (Hedw.) Schimp.												x				
Dicranum sp.				x							x					x
Drepanocladus uncinatus (Hedw.) Warnst.										x				x	x	
Drepanocladus sp.											x					
Hepaticae sp.			x													
Hylocomium splendens (Hedw.) Schimp.										x	x			x	x	
Hypnaceae sp.	x	x	x	x	x	x	x	x	x	x	x	x	x			x
Hypnum crista-castrensis Hedw.										x						
Paludella squarrosa (Hedw.) Brid.												x				
Pleurozium schreberi (Willd.) Mitt.						x				x	x	x		x		
Polytrichum piliferum Hedw.										x				x	x	
Polytrichum sp.	x		x	x	x	x	x			x	x			x		x
Ptilidium ciliare (L.) Nees.										x				x	x	
Rhytidiadelphus sp.										x						
Sphagnum sp.			x	x							x	x				
LICHENS							x		x		x					
Alectoria nigricans (Ach.) Nyl.				x							x					
Alectoria ochroleuca (Hoffm.) Mass.				x									x			
Baeomyces sp.				x												
Certaria cucullata (Bell.) Ach.				x							x		x	x	x	
C. islandica (L.) Ach.				x			x				x		x	x	x	
C. juniperina (L.) Ach.													x			
C. lacunosa Ach.													x			
C. nivalis (L.) Ach.													x		x	
C. richardsonii Tuck.														x		
C. tilesii Tuck.				x												
Cetraria sp.													x			
Cladonia alpestris (L.) Rabenh.							x				x			x		?
C. amaurocraea (Floerke) Schaer.				x										x	x	
C. bellidiflora (Ach.) Schaer.																x
C. cornuta cylindrica Schaer.														x	x	
C. delessertii (Nyl.) Vain.														x	x	
C. gonecha (Ach.) Asahina														x	x	
C. gracilis (L.) Willd.															x	x
C. gracilis chordalis (Floerke) Schaer.														x		
C. gracilis elongata (Jacq.) Floerke														x		
C. macilenta Hoffm.														x		
C. macilenta squamigera Vain.															x	
C. mitis Sandst.															x	
C. pleurota (Floerke) Schaer.														x	x	
C. rangiferina (L.) Web.				x			x				x		x	x	x	x
C. sylvatica (L.) Hoffm.											x	x	x	x	x	?
C. uncialis (L.) Web.															x	
C. verticillata (Hoffm.) Schaer.														x	x	
Cladonia sp.				x	x				x							x
Cornicularia divergens Ach.													x			
Dactylina arctica (Hook.) Nyl.													x			
Lobaria varrucosa (Huds.) Hoffm.															x	
Lobaria sp.																x
Nephroma arcticum (L.) Torss.														x	x	
Ochrolechia frigida (Sw.) Lynge													x	x	x	
Parmelia omphalodes (L.) Ach.													x			
Peltigera aphthosa (L.) Willd.																x
Peltigera sp.					x											
P. rufescens (Weis.) Humb.							x									
Pertusaria coccodes (Ach.) Nyl.														x	x	
Pilophorus cereolus (Ach.) Th. Fr.														x	x	
Sphaerophorus globosus (Huds.) Wainio													x	x		
Sphaerophorus sp.				x												
Stereocaulon tomentosum Fries							x							x	x	
Thamnolia vermicularis (Sw.) Schaer.				x							x			x	x	

VEGETATION OF THE CREOSOTEBUSH AREA OF THE RIO GRANDE VALLEY IN NEW MEXICO[1]

J. L. Gardner[2]

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INTRODUCTION

The valley of the Rio Grande in New Mexico is bordered by a narrow belt of brush dominated mainly by creosotebush (*Larrea divaricata*) nearly as far north as the mouth of the Rio Puerco. This area is one of sparse vegetation and low rainfall. Part of the precipitation, however, falls as intense storms, resulting in flash floods from arroyos. These flash flows cause appreciable damage to highway and irrigation installations and to crops and agricultural land in the valley. The information presented in the present paper was collected during the course of investigations on arroyo control along the Rio Grande. It is derived from notes and measurements made in the shrub belt from Las Cruces, New Mexico, as far north as creosotebush is prominent in the vegetation, a distance of approximately 170 miles (Fig. 1).

The vegetation of the area nearly as far north as San Marcial was regarded by Shreve (1942) as Chihuahuan Desert. Clements and others, on the other hand, have considered it to be Desert Plains Grassland, with the shrub-dominated areas representing grazing disclimax or successional stages (Clements 1934; Clements & Shelford 1939; Cooperrider & Hendricks 1937; Weaver & Clements 1938; Wooton 1922). Clements (1944) regarded this part of the area as belonging to the driest of three faciations of the Desert Plains Grassland in the United States. Although, if the writer interprets the different concepts correctly, a part of the difference lies in definition of the term *desert,* part seems to lie in different concepts of the nature of the climax vegetation in the area.

Fig. 1. New Mexico. Study area is a narrow band along the Rio Grande between Las Cruces and the mouth of the Rio Puerco.

GEOLOGY AND SOILS

The Rio Grande flows through a structural depression comprised of a series of basins, which were "formed chiefly by faulting and other deformation of the older rocks and subsequent filling with sedimentary and volcanic deposits" (Bryan 1938). These basins are connected by constrictions and canyon sections of varying lengths. Bryan likened the system to a stream flowing from one sand-filled tub

[1] Contribution of the Soil Conservation Service, Research Division, U. S. Department of Agriculture, in cooperation with the New Mexico Agricultural Experiment Station, State College, New Mexico.

[2] Soil Conservationist.

to another. The basins are filled to great depths with unconsolidated or slightly consolidated sands and gravels, in which the river has cut an inner valley 250 to 500 feet in depth and one to four miles wide. Bryan (*l.c.*) and Lee (1907) considered the older strata of these basin deposits as belonging to the Santa Fe formation of Pliocene age, and these strata in turn to be overlain by Pleistocene sands and gravels. Flanking the inner valley are terrace plains that slope up to the hills and mountain ranges that border the depression at rates of 50 to 100 feet to the mile. In the section of the present studies, these plains are dissected by a few tributaries that rise in the flanking mountain ranges, and by numerous arroyos that rise on the plains and spill into the river or upon the floor of the inner valley. The longer tributaries are intermittent in their lower reaches, although some of them are perennial near the source. The shorter arroyos are ephemeral, but occasionally spill damaging flows upon the valley floor.

Soils of the area are highly variable, ranging from clay to localized areas of dune sand. In many of the tributary valleys and upland swales, the soil is moderately heavy; in others it is sandy. On the ridges and slopes between these swales and valleys, gravelly soils predominate except in a few areas of deep sand. They range from gravelly sands to gravelly loams and in many places are underlain by caliche. These deposits of calcium carbonate lie at depths of a few inches to a few feet over considerable areas and range in thickness from "a mere impregnation of the soil to a layer of compact limestone 2 to 15 feet thick" Bryan (*l.c.*). A surface pavement of small stones is a common phenomenon (Fig. 2). Owing to low moisture content and high temperatures, organic matter content of the soils is low; it ranges from 2 percent or less in the valley to less than 1 percent on the upland. Several soil series have been named in the valley and along its edges (Nelson & Holmes 1914; Poulson & Fitzpatrick 1929; Sweet & Poulson 1930), and several others have been tentatively proposed for the upland (Unpublished material in the Office of the State Soil Scientist, U. S. Soil Conservation Service, State College, New Mexico). Judging from the write-up sheets of the latter, however, there is little correlation between soil series and dominant vegetation—*e.g., Larrea divaricata* is given as the dominant vegetation on no less than six and *Flourensia cernua* on three. Consequently, no attempt will be made to give names of series. From evidence to be presented, it is the writer's belief that the top soil has been removed from rather wide areas of the upland terraces.

CLIMATE

The climate of the area is arid (Thornthwaite 1941). Average annual rainfall ranges from a little more than 8.5 inches at State College and San Marcial to slightly more than 10 inches at Socorro. On the average, two-thirds to three-quarters of the precipitation falls between April 1 and September 30, and approximately half (47 to 60 percent) in July, August, and September. There is a wide difference between the wettest and the dryest years. Thus, in the vicinity of the Agricultural College, 3.49

FIG. 2. This is the area described by Emory (1848) as grass-covered. Note stalked condition of the tarbushes. The lack of grass, the presence of creosotebush and tarbush, and the erosion pavement are typical of many square miles of the table-lands that border the valley.

inches of moisture fell at Fort Seldon in 1873 (Linney and Garcia, 1918), contrasted with 19.61 inches at the College, 10 miles to the south, in 1941. Values approaching these extremes appear throughout the record. Similar differences are to be found in the records of the other stations. Summer rainfall is spotted, and often the storms are torrential; winter precipitation is more general and less intense. Snowfall is occasional and light.

Evaporation is high. Annual averages from 48-inch land pans of Weather Bureau Class A installations in or near the valley are: 104.2 inches at Elephant Butte Dam near Hot Springs; 114.2 inches at Caballo Dam, which is 20 miles south of Hot Springs; 94.6 inches at the Jornado Experimental Range, 25 miles northeast of Las Cruces; and 92.4 inches at State College, 3 miles southeast of Las Cruces. Evaporation is highest in June; during this single month it exceeds mean annual precipitation at these stations by approximately 50 percent. Calculated annual evaporation from Elephant Butte reservoir is 6.0 feet (National Resources Committee, 1938), and that for June alone slightly exceeds the mean annual precipitation.

Summers are hot. Mean temperatures for July, the hottest month, are 78° F. or above at all stations. Monthly means for June, July, and August are all 75° F. or above, but the highest temperature of record at State College is only 109° F. and that of Socorro is 108° F. Winters are mild; below-zero temperatures are infrequent, although in many winters the temperature may drop below +10° F. at night for short periods of time. December and January are about equally cool, but the lowest mean for either month at any of the stations in the study area is 37.6° F. at Socorro. Length of growing season ranges from an average of 206 days in the southern to one of 198 days in the northern part of the area, the duration being from early April to late October. No recent compilations of wind velocities are available, but drying winds of considerable velocity are common from February or March well into June. These spring winds not only dry out the soil, but cause much soil movement in the form of dust and sand storms.

EARLY DESCRIPTIONS OF VEGETATION

The upper Rio Grande valley has been known to Europeans since the Spanish explorations of the 16th century. The Spanish explorers, however, appear to have made few comments on the vegetation. Espejo, in the account of his journey of 1582, mentioned mesquite groves, prickly pears, and (on the mountains) "nutpines, sabines, and cedars," and said that along the banks of the river he found "many groves of white poplar" and "thickets of grape vines and Castilian walnut trees" (Bolton 1916); but Oñate, who led a colonizing expedition up the river in 1598, and others mentioned only plants cultivated or used by the Indians (Translations consulted: Bolton 1916; Hammond 1926). Oñate, however, brought with him to New Mexico 7,000 head of cattle, sheep, horses, and mules (Hammond 1926), which had to be maintained by grazing along the way.

In March, 1807, Zebulon Pike marched down the Rio Grande on his way from Santa Fe to Chihuahua. In his journal (Pike 1811), his description of the country is vague; but to the south of the present Caballo Dam and 3 miles east of the river, he described the country as "a large flat prairie." Much of this area is now brush covered. Josiah Gregg covered much of Pike's route in 1839. Of the country between Juarez, Chihuahua, and Socorro, New Mexico, he wrote (Gregg 1845): "The valleys are timbered with cotton wood, and occasionally with *mezquite*, which, however, is rarely found higher up than the lower settlements of New Mexico [Socorro, Polvadero, etc.] . . . The plains and highlands generally are of a prairie character, and do not differ materially from those of all Northern Mexico, which are almost everywhere completely void of timber." Elsewhere in the same publication, he wrote: "The High prairies of all Northern Mexico . . . [are] mostly clothed with different species of a highly nutritious grass called *grama*, which is of a very short and curly quality." At that time, of course, Northern Mexico included New Mexico. Concerning mesquite, Wislizenus (1848), in contrast to Gregg's description of its occurrence as occasional, wrote; "[It] is no doubt the most common tree in the high plains of Mexico." In the Botanical Appendix of Wislizenus's account, Engelmann, to whom the botanical collection was turned over, wrote that creosotebush was first collected at Olla (La Jolla), which is a short distance south of the mouth of the Rio Puerco and across the Rio Grande, and that the shrub was common from there south. He made the same notation, however, concerning *Chilopsis linearis*. Wislizenus himself not only did not mention creosotebush in his account, but, two days after the plant was first collected, he wrote: "The vegetable creation in the valley of the Rio del Norte, characterized principally by a great many sand plants, exhibits since a couple of days two specimens of shrub, which for their extension over the greatest part of Mexico, and their daily appearance hence, deserve particular notice. The one the so-called *mezquite*, a shrub belonging to the family of Mimmoseae, and a species of algorobia. . . . The other new companion to which I allude is the *yucca*, resembling in appearance the palm tree, and therefore commonly called palmilla. . ." To one familiar with the area, it seems incredible that, if creosotebush had been as abundant and nearly universal along the route then as it is now, it could have escaped mention by both Wislizenus and Gregg or that Wislizenus could have selected two other plants—one of which was *Yucca elata*—for particular mention because of their abundance and widespread distribution. Another now common shrub that was mentioned neither by Wislizenus in his narrative nor by Engelmann in the Appendix is *Flourensia cernua*.

In the fall of 1846, Lieut. J. W. Abert (1848) came down the river to the ruins of Valverde, about 25 miles below Socorro. Opposite the mouth of the Puerco, he wrote in his journal: "Today we saw great quantities of mezquit 'prosopis glandulosa,' and a curious evergreen plant, belonging to the zygop[h]yllaceae, that gives out a very pungent odor, resembling kreosote. It occurs in dense spherical masses, similar to the common box, which, at a little distance, it resembles. . . . It loves a sandy soil, and prefers the hill sides to the plains."

In the fall of 1846, W. H. Emory came down the west side of the river about as far as the present town of Hot Springs before turning west. Just above Socorro, he first encountered creosotebush and mesquite. Of the former, he wrote (Emory 1848) that the "usual growth is the height of a man on horseback." This probably means that he observed it only in very sandy areas, for measurements of several hundred plants between Las Cruces and the northern end of the belt show that the bushes rarely exceed a meter in height except in such areas or in washes. The night after he left the Rio Grande, Emory recorded in his journal: "After mounting to the table land, some 200 feet above the river, it is very level, except where the table land is indented by streams from the mountains, most of which are now dry. . . . On the table land the winter grama (a more delicate grass than the summer grama) was in great abundance, but is now dry and burnt." No mention is made of brush. Today this table-land is brush-covered, and grass is rare (Fig. 2). Also in 1846, Cooke and the Mormon Battalion followed the river down to within about 10 miles of the present town of Hatch before turning west on their way to California. In his journal, Cooke (1848) mentioned at several places that the uplands bordering the river valley were covered with "good," "abundant," or "luxuriant" grama grass, but there is no mention of their being covered with shrubs.

In 1849 R. B. Marcy marched down the river from Santa Fe to Dona Ana, via the Jornado del Muerto, and thence eastward through San Augustine Pass. After he had traveled some 50 to 60 miles from Dona Ana to the Hueco tanks, his journal (Marcy 1850) records: "Along the whole course of the road from Dona Ana here, there has been a most luxuriant growth of grama grass of several different kinds . . ." Marcy made no mention of brush in this part of his route, but J. H. Byrne, Assistant Computor to Pope's party, who followed Marcy's route to the Hueco tanks, wrote in his diary (Pope 1854, Appendix A): "Encamped at sundown on the Jornada [the Tularosa Basin]. No wood nor water; grass plenty. Cooked with the brush that lay around on the plain, sufficient for the purpose." There were 75 men in the party.

Pope (1854) alluded to the "excellent pastoral character of the table lands" bordering both sides of the Mesilla valley, in which Las Cruces and its neighboring towns now lie; and he described the country lying near the 32nd parallel between the Pecos and the Rio Grande as consisting "of elevated table-lands destitute of wood and water, except at particular points, but covered with a luxuriant growth of the richest and most luxuriant grasses known to this continent." This must have been an exaggeration, but it does indicate that grasses were dominant and that shrubs were, at most, sparse.

In describing the table-lands between the isolated mountain ranges of the Border region of Transpecos Texas and southern New Mexico and Arizona, Emory (1857) wrote: "The plains are covered with a scrubby growth, incapable of affording subsistence to any but a class of small animals, such as antelope, prairie-dogs, and rabbits. Most generally however, in the southern part of the United States [which now included New Mexico], these plains are clothed with a luxuriant growth of 'grama,' the most nutritious of all grasses. Sometimes they are destitute of all vegetation except the larrea Mexicana, the yucca, the cactus, and other spinous plants, and are paved with minute fragments of chalcedony, basalt, agate, and other hard rocks." But, again, of the country comprising the Gadsden Purchase the eastern border of which was the Rio Grande: "West as far as 112° meridian of longitude, the soil of the levels and hills is everywhere good, and, except in the playas, covered with a luxuriant growth of nutritious grass, mostly grama."

Beale, with his "Camel Brigade," came up the river from below El Paso in 1857. In describing the Jornada del Muerto plain, he wrote (Beale 1858) that there were "hundreds and hundreds of thousands of acres, containing the greatest abundance of the finest grass in the world, . . ." and that throughout this 90-mile stretch the grass was "everywhere excellent and abundant. . . ." When he struck the river again a few miles below Fort Craig, he recorded: "The grass on the river bottoms is not good, and we therefore camped on the nearest hills to the river, where we found excellent gramma." Today these hills are generally brush-covered and grass cover is sparse or wanting.

Parry (1859), Botanist with the Boundary Survey Commission, wrote of the vegetation of the El Paso basin and the upper Rio Grande valley: "The principal grass of this region consists of the kinds known as 'bunch grass,' and belong to the genera *Chondrosium* and *Bouteloua*. The margin of the table land, where it borders upon the valley, is broken by deep ravines, and we find here upon the sandy bluffs a growth of chapparral, made up principally of mezquit and the equally thorny Acacias." He found on these table-lands the shrub species present today, but made no mention of their abundance.

Fountain (1885) wrote of thousands of tons of grama grass hay that could be cut and baled in close proximity to the railroad. Nor was this done in swales where water concentrated; for "[grama grass] thrives best in sand and gravel and is found in per-

fection on the dry sandy plains and rocky hill slopes." Long-time residents of Las Cruces have told the writer that within their memories grama grass hay was cut and baled in areas now covered with creosotebush or mesquite, and that many of the washes, instead of being raw gullies as they are today, were clothed with grass. The usual explanation for the decrease in grass is that "it doesn't rain as much as it used to." This is, of course, unsupported by the records; and some of my informants —all ranchers—attribute it to over-grazing. Mr. Harold Olson, a resident of Socorro for 25 years, told the writer that long-time residents there had told him that they remembered when the area between the town and Socorro Mountain supported grass "belly high to a horse." Today the shrub cover in this area averages 16 percent, of which 84 percent is creosotebush and 10 percent mesquite; and the basal area of grasses averages less than 0.1 percent cover.

CLIMAX VEGETATION OF THE AREA

Whether one accepts Shreve's hypothesis that the lower two-thirds of the area is Chihuahuan Desert, or Clements' that it is Desert Plains Grassland, there seems, on the basis of descriptions of early travelers and of long-time residents, to be little room for doubt that the grass cover has markedly decreased and the shrubs greatly increased during the past hundred years or less. It would appear that in their original condition the table-lands bordering the Rio Grande were generally grass-covered, with scattered shrubs among the grasses. Shrubs seem to have dominated in particular areas, such as on bluffs and in some very sandy places; but in the present vegetation, the writer has never observed a cover of grass that could be described as "luxuriant," "excellent," or "good" in areas where shrubs even approach dominance.

From the quoted descriptions and the results of the present study, it is the writer's opinion that the climax vegetation of the lower two-thirds of the study area is Desert Plains Grassland, with *Bouteloua eriopoda* and its associates dominating the uplands and *Hilaria mutica* and its associates dominating the shallow swales. The northern third, where *H. mutica* is replaced by *H. jamesii,* probably represents part of a broad ecotone between the Mixed Prairie to the north and the Desert Plains Grassland to the south, with the elements of the latter predominating in this section. Under this hypothesis, shrub-dominated areas represent grazing disclimax or stages in the primary succession.

METHODS OF STUDY

Between 1946 and 1949, measurements were made and notes were taken in the upland vegetation along the Rio Grande from Las Cruces, New Mexico, to within about six miles of the mouth of the Rio Puerco. One set of samples was taken along U. S. Highway 85, which traverses the area lengthwise. Another set comprised 12 transects of samples approximately at right angles to the valley. Along Highway 85, samples were taken at mile intervals, except where the points fell in house- or barn-yards, feedlots, or townsites, or where the road ran through the valley. Such places were skipped. The lines of samples taken at right angles to the river began at the edge of upland vegetation bordering the river or the valley and extended back one station beyond the edge of the brush belt or to the mountains or to the water-shed divide, whichever was reached first. In places the brush gives way to grass before the mountains are reached; in many others, it reaches to the foot of the mountains; and occasionally thin stands of creosotebush and other shrubs extend a short distance up the hillside from the plain. The cross lines were spaced as nearly as possible at 15-mile intervals; but, owing to lack of available roads, the intervals varied from 10 to 25 miles. Samples were taken at mile intervals from the starting point, and the transects varied from 3 miles to 18 miles in length.

Sampling was done by means of the line interception method (Canfield 1941). At each sampling site, the vegetation on two 100-foot parallel lines was measured, and a list was made of additional species found within an approximate radius of 25 yards. Thus the quantitative data presented are based on the measurements, but presence in the sample is based on these and the supplemental notes. The notes included remarks on soil texture, erosion pavement, condition of plants, height of each shrub and half-shrub measured on the lines, exposure, etc. The lines were located with reference to an arbitrarily selected point. When the land was fenced, as along Highway 85, this point was the fence-post next in front of the car, which had been stopped in accordance with the speedometer reading. The first line was opposite this post and normal to the fence; the second was two posts farther along and parallel to the first. To avoid trailing effects along the fence, the lines were located two—sometimes three—steps in from the fence. When the land was open, a point on the car was used as a reference, and the lines were 20 steps apart. Besides the two general sets of samples just described, others were taken under special circumstances, which will be described as the pertinent data are discussed. Unless otherwise noted, each sample always comprised two 100-foot lines and a supplemental list of species present but not measured. In addition to the measured samples, notes were made of the species occurring in 93 washes at the points where they crossed Highway 85, or at other convenient places, between Las Cruces and the Rio Puerco.

On the measured lines, basal area of grasses was measured at the ground level; shrubs and half-shrubs were measured at the widest extent of the crown intercepted by the line, with gaps in the crown of 0.1 foot

or greater omitted; forbs that were rooted on the line were counted. Since the samples were taken at different times of the year, from early spring until late fall, the data for forbs are less representative than those for the other groups, owing to the fact that different parts of the area were sampled at different seasons. Names of grasses are those given in Hitchcock's Manual as revised by Chase (1951). For shrubs the nomenclature of Benson and Darrow (1944) is followed; for other plants, that of Kearney and Peebles (1942). In cases of doubtful identification, specimens were collected and checked against the herbarium of the New Mexico College of Agriculture and Mechanic Arts. Scientific names are given in the tables and at the points where the species are discussed in detail.

PRESENT VEGETATION OF THE UPLANDS

For convenience in presenting and discussing the data, the area has been divided into sections from south to north on the basis of changes in vegetation as revealed by analysis of the samples. South of Hatch, shrubs are more abundant, as is shown by the amount of shrub cover and by the number of species per sample; and there is less grass than in any other section (Tables 1 & 2). North of Hot Springs, mesquite is less prominent than it is to the south. In the interval between 24 miles north of Hot Springs and 29 miles south of Socorro, the grass cover is greater than it is on either side, and the sample at 29 miles south of Socorro was the most northerly on which tarbush was measured to the west of the river. Beyond six miles north of Socorro, creosotebush is dominant only in patches. These distances are as measured along U. S. Highway 85. The data for the different sections and for the area as a whole will be presented and discussed as average percent cover, based on the line measurements; as percentages of the samples occupied by different species and groups of species; and as degree of association of the more commonly occurring species. This method of presentation has been selected as perhaps the simplest that will summarize the unwieldy mass of data and still allow an adequate portrayal of the structure of the present vegetation.

The data showing average percent cover of vegetation appear in Table 1. The species given in this table are those that were measured on 10 percent or more of the samples. Within each section, the data, with few exceptions, show close agreement between the differently oriented transects; and there was equally good agreement in percentages of the samples

TABLE 1. Summary of vegetation in the shrub belt along the Rio Grande valley from Las Cruces north, as measured by transects along and across the valley. Species given are those that were measured on 10 percent or more of the samples.

Portion of valley represented	Transect orientation with respect to valley	GRASSES (basal area, percent cover)						SHRUBS (crown spread, percent cover)						HALF-SHRUBS (crown spread, percent cover)			FORBS (number of plants)
		Bouteloua eriopoda	*Muhlenbergia porteri*	*Scleropogon brevifolius*	*Tridens pulchellus*	All others	Total	*Ephedra trifurca*	*Flourensia cernua*	*Larrea divaricata*	*Prosopis juliflora* varieties*	All others	Total	*Gutierrezia sarothrae*	All others	Total	Total number per 100 ft. subsample
Las Cruces to Hatch (36 miles)	along.....	T**	.01	0	.01	.02	.04	0.4	0.5	10.1	8.1	1.3	20.4	0.1	2.4	2.5	0.06
	across.....	.01	.01	0	.01	.01	.04	0.7	0	7.6	6.7	7.9	22.9	0	1.2	1.2	3.58
	average...	T	.01	0	.01	.02	.04	0.5	0.3	9.1	7.5	4.1	21.4	T	1.9	2.0	1.54
Hatch to Hot Springs (40 miles)	along.....	0	.01	.09	.01	.01	.12	0.2	1.1	8.8	4.0	4.8	18.6	0.3	0	0.3	.28
	across.....	T	.01	T	.02	.09	.13	0.1	1.6	10.1	0.5	1.0	13.3	0.2	0.4	0.6	0
	average...	T	.01	.06	.01	.04	.13	0.1	1.4	9.6	1.7	2.3	15.1	0.2	0.3	0.5	.10
Hot Springs to 23 miles north. (23 miles)	along.....	.09	.01	.18	.10	0	.38	0.3	2.9	9.0	0.9	1.1	14.2	0.2	0	0.2	.20
	across.....	.06	T	.10	T	.09	.26	0.1	3.5	9.5	1.0	0.5	14.5	T	0.3	0.3	.22
	average...	.07	.01	.14	.06	.04	.32	0.2	3.2	9.2	0.9	0.8	14.3	0.1	0.1	0.2	.21
24 miles N. of Hot Springs to 29 miles S. of Socorro (23 miles)	along.....	.29	.03	.07	.19	.14	.72	0.2	0.9	6.2	T	1.1	8.4	0.3	0.1	0.4	.71
	across.....	.14	.03	.26	.01	.12	.56	T	2.4	7.2	0.1	0.2	9.9	0.3	0	0.3	.47
	average...	.23	.03	.15	.12	.13	.66	0.1	1.5	6.6	0.1	0.7	9.0	0.3	0.1	0.4	.61
28 miles S. of Socorro to 6 miles N. of Socorro (34 miles)	along.....	.02	T	.02	.07	0	.11	T	0	10.0	0.1	2.1	12.2	0.1	0	0.1	.65
	across.....	.03	T	.02	.02	.07	.15	0	0.3	10.7	1.2	1.5	13.7	0.1	0.1	0.2	.57
	average...	.02	T	.02	.05	.03	.13	T	0.2	10.4	0.6	1.8	13.0	0.1	T	0.2	.61
7 to 23 miles north of Socorro (16 miles)	along.....	.03	0	.53	.03	.17	.76	0	0	0.5	0	1.4	1.9	0.9	0	0.9	1.28
	across.....	.13	0	.02	.01	.44	.60	0	0	3.6	T	0.7	4.4	1.7	0	1.7	4.50
	average...	.07	0	.35	.02	.27	.70	0	0	1.6	T	1.2	2.8	1.2	0	1.2	2.43

*Mostly *Prosopis juliflora* var. *torreyana*, but some var. *glandulosa*. **T = Trace.

occupied by different species and groups of species. Thus, on the area as a whole, creosotebush was measured on 80 and 83 percent, respectively, of the samples on the transects along and across the valley and was recorded on 84 and 89 percent; corresponding values for perennial grasses were 64 and 64 percent and 77 and 75 percent. Such agreement implies that the two sets of samples furnished equally good estimates of the vegetation of the area, and that, so far as the total cover of the different groups is concerned, either set would have been enough. It implies further that the vegetation does not differ consistently from one edge to the other. The latter implication is borne out by a more detailed analysis of the samples of the cross sections. General field observations, however, indicate that, owing to the stands of mesquite that occupy areas below the escarpment of the main valley and the lower reaches of many of the wider tributary valleys, there is a tendency for mesquite to account for more of the cover at the lower end of the cross sections. This is not invariably the case, however, for very sandy areas farther back may be occupied by this species. There is a tendency also for grass to be more abundant in the last mile or so of the shrub belt on the longer cross-sections.

A few general relations emerge from an examination of the data in Table 1. Grass cover, with the exception of that in the fifth section, increases progressively northward from Las Cruces; shrub cover, except for that in the fifth section, decreases. Higher percentages of shrub cover are associated with lower percentages of grass cover. No such relations are apparent with half-shrubs and forbs, either with respect to other groups or to geographical location. In Table 2 are shown number of species recorded and average number of species per sample in each section of the valley. Number of species, both measured and recorded, in the different groups varied from section to section, but no such geographic pattern as was apparent for cover of grasses and shrubs emerged from these data. On the other hand, average number of species per sample followed the same pattern as that observed for cover: an increase for grasses from south to north and a decrease for shrubs, and no regularity of change for half-shrubs or forbs. Closer examination of the data indicates that the seeming correlation of the average number of species of the grasses and the shrubs with amount of cover may be at least partially fortuitous. Grass cover in both the second and the fifth section was 0.13 percent, but the average number of species per sample was 1.7 in the former and 2.1 in the latter sections; and shrub cover in the third, fourth, and fifth sections was 14.3, 9.0, and 13.0 percent, respectively, but the average number of species was 3.7, 2.9 and 2.7, respectively. The number of species observed on the samples of the three sections was 17, 17, and 22 in the third, fourth and fifth, respectively. It would seem to follow that the lower averages in the fourth and fifth sections were due to segregation of the species into communities, with few species represented, or to the presence of scattered individuals of a number of species sparsely represented. That the latter was the case is indicated by several facts. A high proportion of the shrub cover is due to creosotebush, and creosotebush was dominant or codominant on the great majority of the sampling sites in

TABLE 2. Total number of species and average number per sample (measured and total) in each of the sections of the valley, and on the area as a whole.

Section of valley represented	Method of recording	GRASSES		SHRUBS		HALF-SHRUBS		FORBS		TOTAL	
		Number of species	Average per sample	Number of species	Average per sample	Number of species	Average per sample	Number of species	Average per sample	Number of species	Average per sample
Las Cruces to Hatch	measured...	7	0.6	17	2.7	6	1.0	8	0.5	37	4.8
(36 miles)	total.......	13	1.0	23	5.1	7	1.6	23	1.8	66	9.5
Hatch to Hot Springs	measured...	9	0.9	16	2.6	5	0.3	3	0.1	33	4.0
(40 miles)	total.......	12	1.7	20	4.1	6	0.5	4	0.2	42	6.6
Hot Springs to 23 miles north	measured...	9	1.4	11	2.4	3	0.3	4	0.2	27	4.4
(23 miles)	total.......	11	2.4	17	3.7	3	0.5	9	1.0	40	7.6
24 miles north of Hot Springs to 29	measured...	12	2.3	14	2.1	2	0.5	9	0.7	37	5.7
miles south of Socorro (23 miles)	total.......	13	2.7	17	2.9	2	0.6	12	1.0	44	7.3
28 miles south of Socorro to 6 miles	measured...	15	1.3	22	2.0	3	0.5	16	1.0	56	4.7
north of Socorro (34 miles)	total.......	15	2.1	22	2.7	3	0.8	24	1.7	64	7.2
7 to 23 miles north of Socorro	measured...	14	3.1	4	0.9	1	0.9	9	1.3	28	6.1
(16 miles)	total.......	15	3.6	9	2.0	3	1.3	18	2.5	44	9.4
Entire area	measured...	21	1.4	30	2.2	9	0.5	32	0.5	92	4.7
	total.......	24	2.1	35	3.5	11	0.8	57	1.2	127	7.7

TABLE 3. Species measured on 1 percent or more of the samples along and across the valley or prominent in the washes, together with percentage of samples and sections of the valley in which they were observed. (7 grasses, 7 shrubs, 3 half-shrubs, and 36 forbs that were measured on fewer than 1 percent of the samples were omitted from this table.)

Species	Samples on which measured (percent)	Samples on which measured and observed (percent)	Sections in Which Observed[1]					
			Las Cruces to Hatch	Hatch to Hot Springs	Hot Springs to 23 miles north	24 miles north of Hot Springs to 29 miles south of Socorro	28 miles south of Socorro to 6 miles north of Socorro	7 to 22 miles north of Socorro
GRASSES								
Aristida fendleriana	8.3	10.3	----	----	----	------	------	----
Aristida pansa	1.5	4.7	----	----				
Bouteloua barbata	2.9	4.7	----	----	....	......	------	----
Bouteloua curtipendula	5.9	10.3	----	----	----	------	------	....
Bouteloua eriopoda	18.1	26.5	----	----	----	------	------	----
Hilaria jamesii	7.8	9.8				..--	------	----
Hilaria mutica	7.3	11.8	----	----	----	------	-	
Muhlenbergia porteri	11.8	32.8	----	----	----	------	--	
Muhlenbergia torreyi	2.9	4.4			----	------	------	
Munroa squarrosa	2.4	3.4	----				------	----
Scleropogon brevifolius	27.0	33.3	....	----	----	------	------	----
Setaria macrostachya	1.0	4.4	----	----	----	-		
Sporobolus airoides	2.9	3.4	----	----	....	------	------	--..
Sporobolus cryptandrus	7.8	9.8	....	....	----	------	------	----
Sporobolus flexuosus	2.9	4.7	----	----	....	......	------	----
Sporobolus giganteus	1.0	1.0					------	
Tridens pulchellus	32.0	38.7	----	----	----	------	------	----
SHRUBS								
Acacia constricta	3.4	3.9	----	----	----			
Atriplex canescens	6.3	8.2	----	----	....	------	------	----
Brickellia laciniata	0.0	0.5	xxxx	xxxx	xxxx	xxxxxx	xxxx	
Chilopsis linearis	0.5	0.5	xxxx	xxxx	xxxx	xxxxxx	xxxxxx	xxxx
Condalia lycioides	4.4	6.3	----	----	-			
Dalea formosa	3.4	7.8	----	....	----	------	------	----
Dalea scoparia	2.4	3.4	----				------	----
Ephedra torreyana	7.3	9.8	----	----	----	------	------	----
Ephedra trifurca	10.8	24.5	----	----	----	------	------	....
Fallugia paradoxa	1.5	1.5	xxxx	xxxx	xxxx	xxxxxx	xxxxxx	xxxx
Flourensia cernua	36.8	39.3	----	----	----	------	-	
Fouquieria splendens	2.4	6.8	----	--			..	
Hymenoclea monogyra	1.0	1.5	xxxx	xxxx	xxxx	xxxxxx	xxxxxx	xx
Koeberlinia spinosa	1.5	5.9	----	--				
Krameria parvifolia	1.5	1.5	-					
Larrea divaricata	81.4	86.3	----	----	----	------	------	----
Lycium berlandieri	4.9	8.3	----	----	----	------	------	
Lycium pallidum	2.0	2.9		-	----	......	......	----
Mammillaria macromeris	1.0	4.4	----	-				
Opuntia clavata	1.5	4.4				--	------	----
Opuntia engelmannii	1.0	3.4	----	....	....	......	----	
Opuntia imbricata	1.0	6.3	----	----	----	------	......	....
Opuntia leptocaulis	8.2	17.2	----	----	----	------	------	....
Opuntia macrocentra	2.4	16.7	----	----	----	------	----	
Parthenium incanum	8.3	15.7	----	----	----	------	------	
Prosopis juliflora vars.[2]	21.9	35.3	----	----	----	------	------	----
Rhus microphylla	2.9	10.2	xxxx	xxxx	--xx	xxxxxx	xxxxxx	xxxx
Yucca baccata[3]	1.9	8.2	----	----	----	------	------	....
Yucca elata	3.4	11.8	----	----	----	------	------	----
HALF-SHRUBS								
Coldenia canescens	3.9	3.9	----	----	-		..	
Croton corymbulosus	1.5	3.9	----	----	....	......	......	....
Dyssodia acerosa	7.8	9.7	----	....	----	------	------	
Gutierrezia lucida	3.4	5.3	----	xxxx	x			
Gutierrezia sarothrae	27.9	42.6	----	----	----	------	------	----
Menodora scabra	2.4	3.9	----		----		------	
Suaeda suffrutescens	1.0	1.0	....	....	-		...	
Zinnia pumila	2.4	4.9	----					
FORBS								
Allionia incarnata	1.5	2.9	----	....	....	......	------	----
Aster hirtifolius	3.4	5.3	....	....	----	------	------	----
Bahia absinthifolia	1.0	2.9	----	....	....	......	......	
Boerhaavia wrightii	1.0	2.4	----	xxxx	xxxx	xxxxxx	xxxxxx	
Cassia bauhinioides	1.5	2.4	----	....	....	......	......	----
Chenopodium incanum	1.0	1.0	----					
Cucurbita foetidissima	....	....	xxxx	xxxx	xxxx	xxxxxx	xxxxxx	xxxx
Eriogonum abertianum	1.9	2.9	----	....	....	......	------	----
Eriogonum polycladon	....	....	xxxx	xxxx	xxxx	xxxxxx	xxxxxx	xxxx
Euphorbia albomarginata	8.8	10.3	----	----	----	------	------	----
Hoffmanseggia drepanocarpa	1.0	2.9				--	------	----
Perezia nana	6.9	20.6	----	----	----	------	------	
Salsola pestifer	1.9	1.9	----	....	....	......	------	----
Solanum elaeagnifolium	1.9	3.9	----	----	----	------	------	----
Sphaeralcea spp.	1.9	3.9	----	----	----	------	------	----
Tidestromia lanuginosa	2.4	2.9	----	....	....		------	----

[1]xxx signifies that the species was observed mainly or wholly in washes; ----, recorded on samples; ...., observed in the section but never recorded on samples.
[2]Mainly *P. j.* var. *torreyana* Benson, but some *P. j.* var. *glandulosa* (Torr.) Cockerell.
[3]Includes *Y. b.* var. *macrocarpa* Torr.

all three sections; moreover, four species each in the fourth and fifth sections fell on only one sample, as compared to but one such species in the third section; of the 16 samples on which creosotebush was the only shrub present, 10 fell in the fifth section, four in the fourth, and one in the third; and 13 sampling sites in the fifth section, nine in the fourth, and eight in the third had but one shrub other than creosotebush.

In Table 3 is given a list of the species that were measured on 1 percent or more of the 204 samples of these transects or that were prominent in the washes. Seven species of grasses, seven of shrubs, three of half-shrubs, and 36 of forbs were measured on fewer than one percent of the samples and were omitted from the table. In addition, Table 3 presents the percentage of samples upon which each listed species was measured, the total percentage upon which it was recorded, and the sections of the valley in which it was recorded or otherwise observed. These points will be taken up as the groups and species are discussed in detail.

In Table 4 are given percentages of association of all species that were recorded on approximately 10 percent or more of the samples. These data are the ratios, expressed as percentages, of the number of samples upon which the two species occurred together to the number upon which were recorded those listed in the first column. This is essentially the Association Index of Dice (1945), except for the use of percentages. *Flourensia cernua, Hilaria jamesii,* and *Hilaria mutica* did not extend throughout the area; and, since the object is to present an indi-

TABLE 4. Association of species appearing on approximately 10 percent or more of the samples, expressed as percentage occurrence of the species listed across the top on samples bearing those listed at the side. For *Flourensia cernua*, *Hilaria jamesii*, and *H. mutica*, which did not extend throughout the area, only those samples falling within their respective ranges are considered.

	Ephedra torreyana	*Ephedra trifurca*	*Flourensia cernua*	*Larrea divaricata*	*Opuntia leptocaulis*	*Opuntia macrocentra*	*Parthenium incanum*	*Prosopis juliflora*	*Rhus microphylla*	*Yucca elata*	*Dyssodia acerosa*	*Gutierrezia sarothrae*	*Aristida fendleriana*	*Bouteloua curtipendula*	*Bouteloua eriopoda*	*Hilaria jamesii*	*Hilaria mutica*	*Muhlenbergia porteri*	*Scleropogon brevifolius*	*Sporobolus cryptandrus*	*Tridens pulchellus*	*Euphorbia albomarginata*	*Perezia nana*
Ephedra torreyana	...	21	31	90	5	5	10	32	16	10	21	70†	26	16	53†	25	18	32	21	10	63*	16	21
Ephedra trifurca	8	...	32‡	74§	18	16	6‡	50*	22†	18	8	64†	12	18*	36	17	20	48†	16§	8	46	8	18
Flourensia cernua	5	20‡	...	96†	29*	19	18	25§	14	8‡	12	39	5	12	20	...	20	44	48†	6	42	8	31†
Larrea divaricata	10	21§	55†	....	18	19*	17	33	11	10	12	42	9	10	24‡	24	15	32	32	8‡	40	9	23*
Opuntia leptocaulis	3	26	72*	94	...	31*	17	20‡	11	9	11	34	3	9	11‡	20	25	43	49*	3	29	3	23
Opuntia macrocentra	3	24	56	100*	32*	...	24	35	18	18	12	38	12	9	29	0	7	53†	41	6	38	9	41†
Parthenium incanum	7	10‡	48	97	19	26	...	26	6	13	8	19§	13	19	32	40	0‡	45	19	3	39	3	32
Prosopis juliflora	8	33*	36§	81	10‡	17	11	...	6	17	14	49	8	4	29	29	11	29	21§	4	41	7	21
Rhus microphylla	14	52†	61	90	19	29	10	19	...	35†	14	76†	14	38†	24	33	22	67†	48	5	62*	10	38
Yucca elata	8	38	30‡	75	12	25	17	50	29†	...	5	54	17	11	38	80	5	50	21	8	42	21	21
Dyssodia acerosa	18	18	41	100	18	18	27	27	14	4	...	50	14	5	23	9	5	36	23	23	64*	5	27
Gutierrezia sarothrae	16†	37†	50	84	14	15	7§	40	18†	15	13	...	17	15	39†	44*	29†	28	26	14	59†	17†	23
Aristida fendleriana	24	29	40	76	5	19	19	29	14	19	14	71	...	33†	76†	62*	12	48	14	28†	62*	24*	29
Bouteloua curtipendula	14	43*	50	81	14	14	29	14	38†	14	5	62	33†	...	67†	67	12	67†	29	5	71†	19	24
Bouteloua eriopoda	18†	33	41	78‡	7‡	18	18	39	9	17	9	59†	30†	26†	...	52†	21	46*	24	24†	63†	18*	33†
Hilaria jamesii	15	5	...	65	5	0	10	30	15	20	10	75*	40*	15	55†	...	...	20	55	30	25	40†	15
Hilaria mutica	8	38	70	83	33	8	0‡	25	17	5	4	67†	4	8	33	...	...	42	58†	12	67†	4	29
Muhlenbergia porteri	9	36†	60	85	19	27†	21	31	21†	18	12	36	15	21†	37*	29	17	...	39	8	54†	10	30*
Scleropogon brevifolius	6	12§	76†	91	25*	21	9	22§	15	7	7	34	4	9	19	41	34†	38	...	13	31	6	27
Sporobolus cryptandrus	10	20	50	70‡	5	10	5	15	5	10	25	60	30†	5	65†	50	33	25	45	...	45	20	10
Tridens pulchellus	15*	29	55	89	13	16	15	39	16*	13	18*	65†	16	19†	43†	22	27†	46†	27	11	...	14	19
Euphorbia albomarginata	15	20	40	80	5	15	5	25	10	25	5	75†	25*	20	50*	67†	11	35	20	20	55	...	20
Perezia nana	10	21	60†	98*	19	33†	24	36	19	12	14	48	17	12	43†	27	20	48*	43	5	36	10	...

*P = .05, †P = .01 —percentage greater than that expected from chance association.
‡P = .05, §P = .01 —percentage less than that expected from chance association.

cation of the effect of soil and other site factors rather than differences in geographic range on association of species, only the samples that fell within the respective ranges of these three species were considered in determining their association with other species.

SHRUBS

Shrubs were measured on 96.1 percent of the samples and observed on another 2.9 percent. As measured on these samples, shrub cover averaged 14.0 percent. The greatest number of shrub species measured on one sample was five; there were nine samples with this number of shrub species measured. The greatest number of shrub species recorded (measured and observed) on one sample was nine; three samples had this number, but none of them was among the nine samples upon which five species were measured.

Even in sites dominated by grasses, a few shrubs were usually found. They are sparse, however, on the steep walls of the deeply entrenched tributaries of the river, even though these slopes may have been severely overgrazed. Shrubs on many of the brush-covered slopes of shallower waterways when viewed from a distance give the impression of being more widely spaced than those on more level areas; but, in many cases at least, this is an optical illusion caused by looking more nearly directly at the ground surface over a greater area than is possible when the observer stands among the shrubs and on the same level with them.

Except in washes, three shrubs were generally dominant: creosotebush, mesquite (*Prosopis juliflora*), and tarbush (*Flourensia cernua*). On the area as a whole, these three species made up 86.4 percent of the total shrub cover; and one or more of them appeared on 92.7 percent of the samples and were measured on 86.4 percent of them. A fourth, chamisa (*Atriplex canescens*), was found dominating a few areas along the edge of the river valley either just below the escarpment or in places where the escarpment was lacking and the valley merged gradually with the upland. Even where dominant, chamisa was usually found associated with substantial amounts of other shrub cover. Thus, on the sample supporting the greatest amount of chamisa, cover due to this shrub was 44.5 percent; that due to mesquite was 10.4 percent. On others, creosotebush was conspicuous.

CREOSOTEBUSH

Larrea divaricata is by far the most prevalent species in the area studied. It appears to be the least exacting of the shrubs in its requirements: although it was rarely if ever observed on blow-sand, it was frequently found on other areas of deep sand, on areas of relatively deep heavy soil, on shallow soils underlain by caliche, and in arroyo beds. It was not observed, however, on sites that were not well drained. A few tests were made for the presence of free calcium carbonate in the soil of creosotebush areas. In some places it was found at the surface, but in others it was first encountered at depths of two feet or more.

In sand and in well-watered areas, such as wash channels and bottoms, creosotebushes may reach heights of two meters or more; on shallow soils underlain by caliche, heights range from 50 to 75 centimeters. Fosberg (1940) reported heights of 4 meters in the vicinity of Mesquite, New Mexico, 10 miles south of Las Cruces. The largest plant observed by the writer, however, was a cultivated one approximately 3.3 meters high, which was about a meter taller than the tallest wild plant observed. The average height of the 2813 plants measured on all samples was 81 cm. That of 103 plants growing on samples taken in arroyo beds on the Agricultural College ranch was 130 cm., and the height of 447 plants on samples from adjacent upland averaged 80 cm. There was no correlation between average height and distance north from Las Cruces; but Shreve (1940) reported that, at the north edge of its range in New Mexico, the branches are so depressed from the effects of snow that the shrubs have the aspect of creeping perennials.

Crosotebush was measured on 81.4 percent of the samples and observed on another 4.9 percent (Table 2). On 16.2 percent of the samples, it was the only shrub measured, and the only one present on 7.9 percent. On 2.5 percent, it was the only species represented. No other shrub except *Ephedra trifurca* and *Dalea scoparia* was found unassociated with other shrubs on any of the samples, and no other species occurred alone on any sampling site. Besides being found on the largest number of samples, creosotebush contributed more to the total cover than any other species; this was true in each of the sections except the northernmost (Table 1). Of the total shrub cover (14%) on the area as a whole, it made up 63.0 percent. Corresponding percentages on the length-wise and the cross sections of the area were 61.1 and 65.0, respectively.

Although creosotebush in the Rio Grande valley ranges as far north as Albuquerque and beyond (Benson & Darrow 1944; Shreve 1940), it is not common above the mouth of the Rio Puerco, and it apparently has not changed in this respect in the past hundred years. To the south of this, however, there is evidence that its abundance has increased and that the process is still in progress. Throughout the area, in those places where bodies of creosotebush adjoin grassland with a history of heavy grazing, the bush is advancing into the grassland. This is indicated by the appearance of young bushes slightly beyond the edge of the main body (Figure 3) or by pioneer bushes that act as nuclei around which colonies form well out in the edge of the grassland (Figure 4). Cases were observed in which two or more of these colonies had merged and the old nuclei were still distinguishable. As these colonies thicken, merge with others, and become incorporated in the main body, it becomes increasingly difficult to follow the process and to discern the nuclei; but some instances

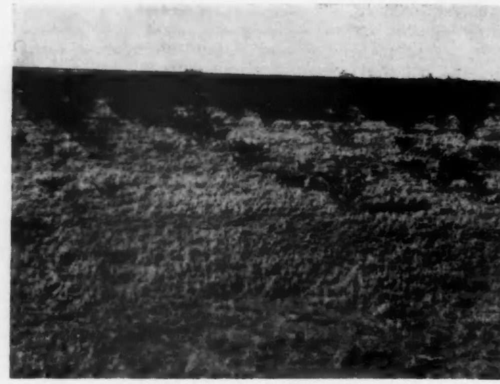

FIG. 3. Invasion of grassland by encroachment of creosotebush along the edge of the main body of shrubs. Grasses in foreground are mainly burro grass, black grama, and tobosa grass.

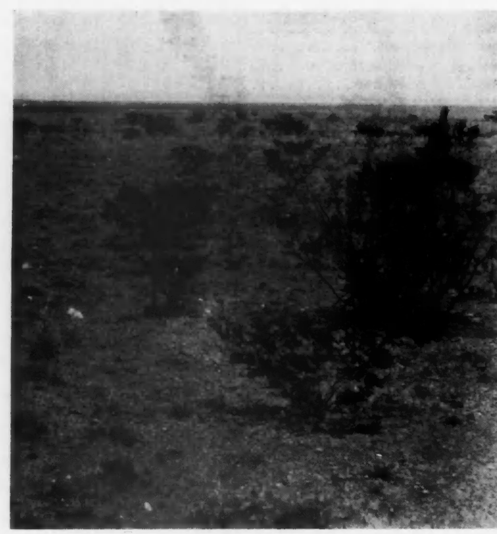

FIG. 4. Invasion of grassland by creosotebush well in advance of main body of shrubs. Note pioneer plant marked by shovel, and smaller plants as marked by hatchet and small pick. Besides the small bushes discernible, there were 5 within a 15-foot radius of the large bush that were a decimeter or less in height.

FIG. 5. A colony of creosotebushes on top of a small hill surrounded by black grama grassland. The soil is shallow. It is the writer's hypothesis that colonies on such sites as this represent the place of creosotebush in the original cover of the area. The presence of small creosotebushes indicates an early stage of deterioration.

were encountered in which the original grasses had all but disappeared and the creosotebush was in control, but in which it was still possible to distinguish the pioneers. On the conservatively grazed grassland of the New Mexico Agricultural College ranch, isolated plants of creosotebush occur in good grassland, but they are apparently not forming colonies (Valentine 1950).

Instances were observed where creosotebushes were growing among black grama (*Bouteloua eriopoda*) plants on shallow soil on the brows of hills surrounded by good black grama grassland (Figure 5). The writer subscribes to the hypothesis that such preclimax sites constituted the original place of creosotebush in the area under study. The presence of small creosotebushes among the still dominant grasses and older shrubs in the picture indicates that the first stages of deterioration have been passed even here, and the shrubs have begun to thicken up. It was possible to trace an entire series of steps from this condition to that in which no grass or only relict clumps were to be found among the dominant creosotebushes. Early steps in this process of deterioration are to be recognized by decrease of grass cover among the shrubs, coupled with erosion of the soil by wind and water; increase of shrubs, as evidenced by little creosotebushes among the larger ones; and increase in size of the creosotebush area by encroachment on the surrounding grassland. This encroachment may or may not be preceded by an invasion of snakeweed (*Gutierrezia sarothrae*). Later stages are marked by virtual or complete disappearance of the grasses; appearance of an erosion pavement; dominance of shrubs over a large area; and, in some instances, loss of soil to the extent that the oldest shrubs seem to have short trunks below the crowns, as is illustrated for tarbush in Figure 2.

Creosotebush accounted for half or more of the shrub cover on approximately 65 percent of the total number of samples and on 75 percent of those upon which the species was recorded. Total shrub cover on these sites averaged 14.1 percent; that of creosotebush, 12.1 percent, or 85.8 percent of the shrub cover. Basal area of grasses averaged 0.13 percent cover, of which 32 percent was due to fluffgrass (*Tridens pulchellus*). To present a list of the species occurring on these samples where creosotebush was dominant would be almost to reproduce a list of the species recorded on the area. Certain exceptions, however, should be noted. Thus, *Chilopsis linearis, Brickellia laciniata, Fallugia paradoxa, Hymenoclea monogyra,* and *Dalea scoparia* were not observed in sites dominated by creosotebush. The first four are common in washes and, with the exception of the fourth, which was observed occasionally also on heavy soil in shallow swales, were rarely observed on the upland except in highway borrow pits and other places where water was concentrated. *Dalea scoparia* and, occasionally, *Chilopsis linearis* were found on areas of deep or shifting sand. With all these species, however, creosotebush was found in lesser amounts, although not in all habitats. Although creosotebush does not attain its best development as a plant on shallow soils, it often occupies such sites almost to the exclusion of other species. Ocotillo (*Fouquieria splendens*) and *Coldenia canescens* were found with it occasionally on ridges closely underlain by caliche in the southern part of the area, and *Dyssodia acerosa*, fluffgrass, and some of the cacti occurred with it on relatively shallow soils here and elsewhere.

TARBUSH

Flourensia cernua, although it was occasionally observed in sandy areas, reaches its best development as a community on heavy soils that receive some extra water. The largest individuals, however were observed in or along washes, although average height of plants along washes did not differ significantly from that of upland plants. It was observed, also, on sandy soil and, infrequently, on shallow soil underlain by caliche. Average height of the 589 plants measured on all samples was 52 cm. Tarbush is usually rejected as forage by all classes of livestock, although Tharp (1944) observed that goats browsed it when nothing else was available, and sheep and cattle may eat it under special conditions.

On the west side of the Rio Grande, the northernmost tarbush plants observed were found in a shallow swale 25 miles south of Socorro. These were the only plants of this species found west of the river and north of the last sample on which it was measured at 29 miles south of Socorro. It ceases to be a prominent component of the vegetation in the vicinity of 35 or 36 miles south of Socorro, although plants are not rare in the intervening distance. To the east of the river, tarbush was observed just north of U. S. Highway 380, which extends east from San Antonio, 10 miles south of Socorro. Here, it was found growing in sandy soil on the mesa top among creosotebush, *Lycium berlandieri, Parthenium incanum,* and snakeweed. Approximately eight miles east of the river on the same highway, it was found growing as a

narrow band on heavy soil at the foot of an escarpment.

Tarbush was measured on 36.8 percent and observed on another 2.5 percent of the total number of samples (Table 2). Within its range, however, it was measured on 47.2 percent of the samples and observed on another 3.1 percent. Of the total shrub cover on the area as a whole, tarbush accounted for 8.7 percent. Total shrub cover within the range of tarbush averaged 14.7 percent. Tarbush made up 10.3 percent of this—an average of 1.5 percent cover. At none of the sampling sites was it observed in the complete absence of other shrubs, although at a few sites other shrubs were sparsely represented.

Tarbush accounted for half or more of the shrub cover on 9.4 percent of the samples within its geographic range and on approximately 18 percent of the samples upon which it was recorded. Basal area of grasses averaged 0.53 percent cover; crown cover of tarbush averaged 8.8 percent; that of total shrubs, 13.9 percent. Within the same geographic range, on the 62 samples upon which creosotebush accounted for half or more of the shrubs, and upon which the shrub cover was comparable in amount, similar averages were: grasses 0.13 percent, creosotebush 11.9 percent, and total shrubs 14.4 percent. Thus, where the total amount of shrub cover was comparable, grass cover on tarbush sites was usually greater than it was on sites dominated by creosotebush or other shrubs. On the tarbush group of samples, the least amount of grass measured was 0.06 percent, and the greatest was 1.58 percent; whereas on 29 samples of the creosotebush group no grass was measured, and the greatest amount was 0.77 percent. On the former group, burro grass (*Scleropogon brevifolius*) accounted for approximately 60 percent of the grass cover (basal area), but for only 41 percent of that on the latter. Fluffgrass made up only 2.5 percent of the grass on the tarbush group but 31 percent of that on the creosotebush group, and tobosa grass (*Hilaria mutica*) amounted to 15 percent of the grass on the former and to but 2 percent of that on the latter group.

Campbell (1931), in his study of succession on clay soils on the Jornada Experimental Range, found that in his Flourensia-Hilaria association, which had a reconnaissance plant density of 0.4, total shrubs accounted for 20 percent and tarbush for 17 percent of the plant cover. Although data for grass cover obtained by the reconnaissance method are not directly comparable with those of the present studies, those for shrubs should be so. Upon this assumption, Campbell's estimate of shrub cover would approximate 8 percent, and that for tarbush 7 percent. Comparison of these percentages with those given above suggests that, with a history of heavy grazing, tarbush has increased some and other shrubs have increased or invaded. This suggestion is given weight by the observation that, in sites—not sampled—with a relatively good grass cover, tarbushes were noticeably less numerous; and in those where grass had obviously decreased, young tarbushes of different ages were present.

Thirty species were recorded on the sampling sites dominated by tarbush. This number is much smaller than that of the species recorded on sites dominated by creosotebush; but on a similar number of samples selected at strict random from those upon which creosotebush was dominant, the number of species was 38. An alphabetical list of the species on tarbush sites follows (those followed by (m) were measured):

Aristida fendleriana (m)	*Larrea divaricata* (m)
Aster hirtifolius (m)	*Lycium berlandieri* (m)
Bouteloua curtipendula (m)	*Menodora scabra* (m)
B. eriopoda (m)	*Muhlenbergia porteri* (m)
Chamaesarcha conioides (m)	*Opuntia imbricata*
Dyssodia acerosa	*O. leptocaulis* (m)
Ephedra trifurca (m)	*O. macrocentra* (m)
Eriogonum abertianum (m)	*Parthenium incanum*
Euphorbia albomarginata (m)	*Perezia nana*
Eurotia lanata	*Prosopis juliflora* (m)
Flourensia cernua (m)	*Rhus microphylla* (m)
Gutierrezia sarothrae (m)	*Scleropogon brevifolius* (m)
Hilaria mutica (m)	*Sporobolus cryptandrus*
Hymenoclea monogyra (m)	*Tridens pulchellus* (m)
Koeberlinia spinosa	*Yucca elata*

A commonly held notion among residents of the region is that the soil requirements of tarbush and creosotebush are so different as to preclude extensive mixing of the two. Some go so far as to say that, in some instances at least, the tension line between areas of the two species is perfectly sharp. Neither data from the samples nor numerous examinations of ecotones bear out such an idea. Of the 80 sampling sites supporting tarbush in the series along and across the valley, 96 percent had creosotebush growing on them in all degrees from dominance of the one species to dominance of the other. The chi-square test for independence (Dice 1945; Snedecor 1946) indicates that the two species are associated more often than would be expected from the hypothesis of chance mixing, chi-square being significant at the 1 percent level of probability. This highly significant value of chi-square is interpreted as supporting the conclusion, drawn from field observations discussed below, that creosotebush is well advanced in its invasion of tarbush areas. The samples upon which half or more of the shrub cover was due to tarbush supported an average of 4.2 percent cover of creosotebush; on the comparable samples upon which creosotebush comprised half or more of the shrub cover, tarbush averaged 1.7 percent cover.

Examination of ecotones indicated that creosotebush is invading the tarbush areas. Young creosotebushes were to be found growing in the edge of the tarbush area, whereas old tarbushes, with very few if any young ones, were to be found in the edge of the creosotebush area. The farther one went into the creosotebush area, the older and less vigorous were the tarbushes, until they were little more than stumps. In places, these tarbush relicts extended to the top

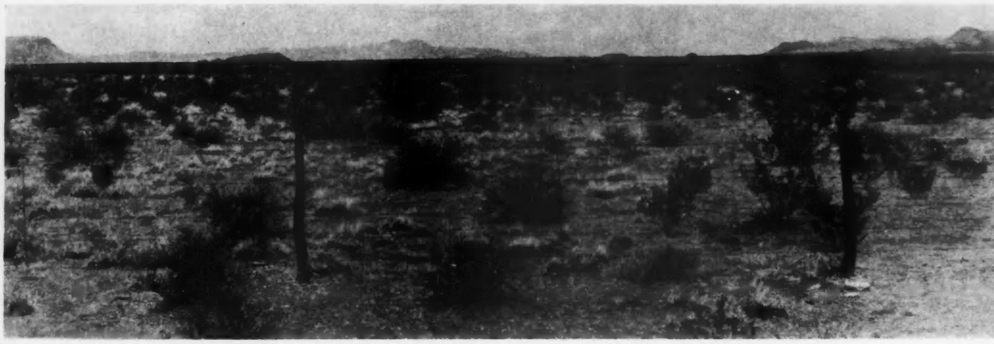

FIG. 6. A tarbush site. The grasses are tobosa grass and burro grass. Note small colony of creosotebushes in lower right foreground.

of the ridge between swales. There were also evidences of erosion on the creosotebush side of the ecotone. On the tarbush side, there was always some grass among the bushes (Figure 6), and the bushes branched from the ground level. Back from the ecotone on the creosotebush side, the grasses soon disappeared, and the tarbushes appeared to have trunks because of the soil's having washed away from the roots (Figure 2). There was, also, an accumulation of small stones on the soil surface. Both of these conditions became more evident with increasing distance from the ecotone. The data of Cooperrider and Hendricks (1937) support the hypothesis of soil removal. These authors found that, in the shrub areas above Elephant Butte dam, an average loss of 29 percent of the cover of vegetation was accompanied by "advanced erosion," which they considered to be a loss of one to two inches of soil; and they found it necessary to go outside of this area to find undeteriorated vegetation for comparison. Their estimate of undeteriorated vegetation in this type was 28 percent cover of grasses, 2 percent cover of forbs, and 5 percent cover of scattered shrubs. All these percentages were based on crown spread of the plants.

As in the case of invasion of grassland by creosotebush, another method of invasion is the formation of colonies around solitary creosotebushes acting as pioneers (Fig. 6).

MESQUITE

Prosopis juliflora is represented in the study area by two varieties, *P. j.* var. *torreyana* and *P. j.* var. *glandulosa*. The former variety is the more common one in the area (Benson 1941); but, in view of the fact that the two intergrade and that some of the samples were taken in the spring before the leaves were fully out or in the fall after they had dropped, no attempt at separation was made, and the data include measurements of both varieties.

Mesquite was measured on 21.9 percent of the sampling sites and was present on another 13.4 percent. It accounted for 14.7 percent of the shrub cover, averaging 2.1 percent cover on the area as a whole. Mesquite is more prominent south of Hot Springs than it is to the north of this point (Table 1). Between Las Cruces and Hot Springs, it was present on 52 percent of the samples and accounted for 21 percent of the shrub cover. Throughout the area of study, scattered individuals were observed in sites dominated by creosotebush, but only on decidedly sandy soil. Of the total number of sampling sites on which mesquite was present, creosotebush was found on 81 percent. Conversely, mesquite was present on 33 percent of the sites where creosotebush was found (Table 4). The chi-square test for independence indicates that the two species are mixed in about the proportion to be expected from chance assortment; and the same is true for the samples below Hot Springs. To one familiar with the area, this result is unexpected, for, especially below Hot Springs, the two species form distinct communities occupying apparently characteristic sites. The samples show, however, that plants of the one species often occur in communities of the other. Since this method of testing association takes no cognizance of abundance of individuals of the species on the sample (Dice 1945), it might be objected that isolated plants receive undue weight and therefore contribute to the apparent discrepancy between field impressions and the implication of the test; but similar testing of the measured portions of the samples, which could be expected to have fewer isolated plants falling on them, produced an even lower chi-square value.

Of the samples upon which mesquite was found within the geographic range of tarbush, the latter appeared on 36 percent. This percentage was significantly lower than the expected; probability was beyond the 0.1 percent level. This was consonant with the fact that tarbush was found more often on heavy soils and mesquite on lighter soil phases; although it is often found on heavy soil in the main valley.

Mesquite made up half or more of the shrub cover on 6.9 percent of the total number of samples and on 19.4 percent of those upon which the species was observed. The sites were all encountered south

of Hot Springs, and they accounted for approximately 20 percent of the samples in this area. Basal area of grasses amounted to 0.04 percent cover, as compared to 0.13 percent on creosotebush sites and 0.53 percent on those dominated by tarbush. Shrub cover on mesquite sites averaged 23.4 percent; that of mesquite, 18.6 percent, or 79 percent of the shrub cover. Thus, the amount of shrub cover was considerably higher on these sites than it was on those dominated by creosote or tarbush, but the percentage of it that was due to mesquite, while markedly higher than that due to tarbush, was not very differfrom that due to creosotebush on their respective sites. Comparison of the list of species recorded on the mesquite sites with that of species observed on tarbush sites shows a number of discrepancies, but several of these species were recorded only once or twice in the total number of samples, so that their appearance on one list and not on the other is difficult of interpretation. The alphabetical list follows:

Allionia incarnata (m)
Aristida sp. (m)
Astragalus sp. (m)
Atriplex canescens (m)
Boerhaavia wrightii (m)
Bouteloua curtipendula
B. eriopoda
Brickellia laciniata
Cassia bauhinioides (m)
Condalia lycioides (m)
Croton corymbulosus (m)
Dalea scoparia
Datura meteloides
Ephedra torreyana (m)
E. trifurca (m)
Euphorbia albomarginata (m)
Flourensia cernua (m)
Gutierrezia lucida (m)
Gutierrezia sarothrae (m)
Haplopappus pluriflorus
Hilaria mutica
Ibervillea tenuisecta
Koeberlinia spinosa (m)
Larrea divaricata (m)
Lycium torreyi (m)
Muhlenbergia porteri (m)
Opuntia engelmannii
O. leptocaulis
O. macrocentra (m)
Parthenium incanum
Pectis angustifolia (m)
Setaria macrostachya
Suaeda suffrutescens (m)
Tidestromia lanuginosa (m)
Tridens pulchellus (m)
Verbesiana encelioides
Yucca elata (m)

No evidence was observed indicating active invasion of creosotebush or tarbush areas by mesquite; it was, however, found invading sandy areas of grassland, with or without the formation of dunes. Invasion is accomplished more by the establishment of pioneers for some distance beyond the main body of mesquite, with subsequent thickening of the stand, than by slow encroachment along its edge. Although invasion by mesquite or other shrubs is usually imputed to misuse of the grassland, Norris (1947) found that mesquite was increasing on a lightly grazed area of semidesert range on the College Ranch; on a transect 1 rod wide extending from the edge of the mesquite type into the grassland for approximately 100 rods, the number of mesquite plants increased from 72 to 155 during a period of 7 years. Invasion of this sort and the appearance of mesquite around watering places and along trails is often ascribed to animals' ingesting the seeds and subsequently dropping them (Campbell 1929; Tharp 1944); and overstocking, by reducing competition with the dominant grasses, would certainly release the resulting young mesquite plants and thus hasten deterioration of the grassland and dominance by mesquite.

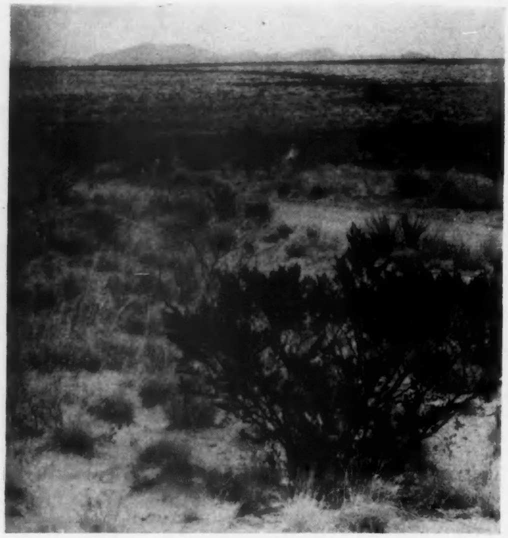

FIG. 7. Strip of mesquite along the old Camino Real. It is the dark streak curving from the midground into the left background.

Old ranchers have told the writer that in early days it was a common practice to carry a bag of mesquite pods to feed horses, much as the farmers of the Midwest carried corn. This could be expected to contribute to the dissemination along trails and wagon roads. An excellent example of mesquite invasion along an old road is depicted in Figure 7. This road was the Camino Real, or King's Highway, which ran from Chihuahua to Santa Fe. The picture was taken at the lower end of the Jornada del Muerto.

Jardine and Forsling (1922) and Campbell (1929) attributed formation of mesquite dunes to the breaking up of grassland by trampling of livestock on over-stocked ranges. Removal of tops and loosening of the soil allows the wind to pick up the soil from around the grass roots and deposit it around the mesquite. Campbell (*l.c.*) pointed out that once a range has reached the dune stage it is very difficult to bring back. During a three-year period of conservative grazing and ample rainfall, however, he was able to trace the stages in recovery from dunes back to the black grama climax, although not the continuous process from inception to completion.

MEXICAN TEA

Ephedra trifurca accounted for but 0.9 percent of the total shrub cover and was never dominant in the vegetation; but it was measured on 10.8 percent of the samples and was recorded on another 13.7 percent. On 1 percent of the samples, it was the only shrub recorded. It may occur in undisturbed grassland, and—unlike the three shrubs just discussed—it does not seem to increase markedly when the range is over-stocked. Of the samples upon which Mexican

tea was found, creosotebush occurred on 74 percent and mesquite on 50 percent; and of those within its geographic range, tarbush appeared on 32 percent. Association with creosotebush and with tarbush fell short of the expected values, probability being at the 1 percent level in the former case and at the 5 percent level in the latter. That with mesquite was significantly greater than the expected (Table 4). This pattern of mixing with these three shrubs suggests that Mexican tea is found more often on the deeper sandy soils, and this is often, but by no means always, true.

Taken as a group, one or more of the four shrubs just discussed were measured on 89.3 percent of the samples and appeared on a total of 94.7 percent; they made up 87.3 percent of the shrub cover.

OTHER SHRUBS

The remaining one-eighth of the shrub cover was contributed by 31 other shrub species, the combined average cover of which amounted to 1.8 percent. In the different sections of the valley, these 31 shrubs accounted for varying percentages of the shrub cover, ranging from 5.6 percent of it in the section just north of Hot Springs to 19.2 percent in that between Las Cruces and Hatch. Members of the group were measured on 48.1 percent of the samples and appeared on another 21.9 percent; they were unaccompanied by any of the other four on 2.9 percent. No member of the group was measured on as many as 10 percent of the samples, and only six were recorded on 10 percent or more.

Certain of these shrubs are dominant, or at least prominent, in a few areas. As was mentioned above, one of these is chamisa, which forms communities in places along the edge of the valley. It is found also among mesquite dunes, often growing on the dune itself among the mesquite stems. Another is white thorn (*Acacia constricta*). To the east of Las Cruces a band of this shrub two to three miles wide lies between bands of creosotebush above and below it. Near the middle of the band, white thorn grows almost to the exclusion of other shrubs, with a cover approximating 25 percent. In rather wide strips along the two edges, creosotebush grows with the white thorn in varying degrees of mixture, from scattered bushes of the former at the inner to scattered bushes of the latter at the outer edges. The underlying factors that account for the presence of this band must await further investigation for their determination. There is no observable soil change that would account for it. Although there appears to be more free lime in the soil than in that of the upper band of creosotebush, there appears to be less than in the soil of the corresponding band below. Ratany (*Krameria parvifolia*) extends from the lower band of creosotebush, through the white thorn, and well into the creosotebush above. A third shrub that is locally abundant in a few sites in broom dalea (*Dalea scoparia*). In abundance, it is an indicator of deep sand. In the present studies, it was found in greatest amount on the dunes just north of the Rio Salado, where it was the only shrub observed on the sampling site, and on very sandy wash fans, where it was accompanied by chamisa.

A shrub that was never prominent in the vegetation but appeared on sandy soil in all sections of the valley was Mormon tea (*Ephedra torreyana*). It was measured on 7.3 percent of the samples and was found on a total of 9.8 percent. Of the sampling sites upon which Mormon tea was recorded, creosotebush was found on 90 percent, mesquite on 32 percent, and tarbush, within its geographic range, on 31 percent. These percentages of association are approximately those expected from chance mixing. Mormon tea was never found, however, on sites where tarbush was dominant or codominant.

Another shrub that did not account for much of the cover but was rather common was mariola (*Parthenuim incanum*). Mariola was measured on 8.3 percent and recorded on an additional 7.4 percent of the sampling sites. It was associated with creosotebush on 97 percent of these sites, with mesquite on 26 percent, and with tarbush—within the geographic range of this shrub—on 48 percent. In all three cases association was about that expected from chance distribution. Its association with Mexican tea was less than the expected (Table 4), a result that is consonant with the field observation that it is most often found on shallow soils.

Rhus microphylla was most often observed in washes, but it occurs also on sand and in swales. It was measured on 2.9 percent and recorded on another 7.3 percent of the samples. Its association with creosotebush, mesquite, and tarbush was approximately as expected from chance distribution; that with Mexican tea was greater than expected (Table 4).

Yucca elata was measured on 3.4 percent of the samples and recorded on another 7.3 percent. It forms savannahs with black grama and persists after the grasses have succumbed to over-stocking; thus, it is found in mesquite-dune areas and among creosotebushes. It is found often on the lighter soil phases, as in indicated by its having been observed more often with *Rhus microphylla* and less often with tarbush than would be expected from chance association (Table 4).

The cacti were represented on the samples by nine species, but they were never very abundant at any of the sampling sites. In the southernmost section, however, on a few hillsides that did not fall on the samples, *Opuntia engelmanii* was observed growing in considerable abundance. As a group, the cacti were measured on 14.2 percent and were recorded on another 25.0 percent of the samples. *Optunia leptocaulis* and *O. macrocentra* were the species most often recorded. *O. leptocaulis* was found on 17.2 of the samples and *O. macrocentra* on 16.7 percent; the former was measured on 8.2 percent and the latter on 2.4 percent. Creosotebush was found on 94 percent of the *O. leptocaulis* samples and on all of those supporting *O. macrocentra*. The former degree of association is not statistically significant, while

the latter is significantly higher than the expected. Association of the two species with mesquite and of *O. macrocentra* with tarbush within its geographic range was very nearly that expected from chance distribution. On the other hand, tarbush, within its geographic range, was found on 72 percent of the *O. leptocaulis* samples, which was significantly more than the expected. Although it would seem from their degrees of association with other shrubs that *O. macrocentra* is less exacting in its requirements than *O. leptocaulis,* the two species were found together more often than would be expected by chance: they fell together on approximately a third of the samples occupied by each species, and the value of chi-square was well beyond the 2 percent level of probability. Other species of cacti fell on such small numbers of samples that no attempt has been made to analyze their association with other species. *Mammillaria macromeris* was recorded on sandy soils among creosotebushes in the southern part of the area, but it was not observed more than a few miles above Hatch. In the northern part of the area, *Optunia clavata* was found growing with grass or among creosotebushes as far south as 35 miles below Socorro (Table 3).

Besides tarbush and the two cacti mentioned, a few other shrubs were not observed throughout the area. *Krameria parvifolia* was not observed north of Las Cruces, although Benson and Darrow (1944) show its range as extending north of Albuquerque. Little and Campbell (1943), however, did not report it from the Jornada Experimental Range, and Wooten and Standley (1915) gave its range as the southern part of the state. *Koeberlinia spinosa* dropped out between Hatch and Hot Springs, and *Condalia lycioides* and *C. spathulata,* respectively, 23 miles above and just below Hot Springs. The maps of Benson and Darrow (*l.c.*) show that these species extend somewhat farther north, and it is highly probable that this is correct. On the other hand, as shown by the present studies, tarbush extends almost to central Socorro County instead of stopping in northern Sierra County, as shown by these authors.

GRASSES

Although grasses were measured on 64 percent and recorded on an additional 12 percent of the sampling sites, average basal area was low in all sections. This was especially true in the southernmost, where basal area of grasses averaged only 0.04 percent cover. From this amount it ranged to 0.68 percent cover in the northernmost section (Table 1). Measurements in protected areas of good grassland in both of these sections gave values of 2.5 percent to 4.5 percent cover. As a group, the grasses were recorded on 74 percent of the creosotebush samples, on 71 percent of the mesquite samples, and on 83 percent of the tarbush samples. Association with the creosotebush and the mesquite was approximately that expected on the hypothesis of random assortment; that with tarbush exceeded the expected by a highly significant amount. When only those samples on which one of these three shrubs made up half or more of the shrub cover were considered, the same pattern was apparent. Similar comparisons were made of the association of these three species with combined grasses other than fluffgrass; *i.e.,* when samples upon which this was the only grass were omitted from the grass samples. These comparisons were made with total number of samples supporting each of these shrubs, respectively, and with those upon which half or more of the shrub cover was due to one of them. The pattern was the same for both types of comparison: association of the grasses with creosotebush was significantly less than the expected value; that with tarbush was very significantly greater than the expected; and that with mesquite was approximately equal to it. When fluffgrass and black grama were similarly omitted from the group of grasses, association of the remainder with creosotebush was still significantly less than the expected value. This comparison was not made with the other two shrubs. Omission of burro grass from the group and comparison of the remainder with tarbush showed that association of the shrub with the remainder of the grasses was very significantly greater than that expected.

Each of four species was measured on 10 percent or more of the samples (Table 1); and each of six others was recorded on approximately 10 percent or more (Table 3). The largest number of grass species measured on one sample was 7, and this was also the largest number recorded. This number of species fell on two samples; but they were situated in the northernmost section, where the samples fell upon sites upon which shrubs were very sparse. On sites where shrubs were dominant, the largest number of grass species measured on one sample was 4, of which there were seven samples; the largest number recorded was 5, and again there were seven samples bearing this number of species.

FLUFFGRASS

Tridens pulchellus was measured on a greater number of samples than any of the other grasses, but it contributed less to the cover than either black grama or burro grass (Table 1). It was measured on 32.0 percent of the samples and recorded on an additional 6.7 percent. Association of fluffgrass with all the shrubs except Mormon tea and *Rhus microphylla* was approximately that expected on the hypothesis of random assortment; with the two mentioned, it was significantly greater than the expected value.

Fluffgrass is a short-lived perennial with little or no palatability to livestock. In stands of palatable grasses, it is therefore favored by heavy grazing. This is illustrated by data from 12 samples taken above Hot Springs, where the highway intersects lobes of grassland that interdigitate with lobes of the brush belt. The right-of-way had received protection or occasional light grazing for about eight years and thus afforded a contrast with adjacent heavily

grazed range. Each sample was comprised of two 100-foot lines that extended 50 feet on each side of the fence. Total basal area of grasses averaged 2.60 percent cover on the protected parts of the samples and 1.11 percent on the grazed parts. Basal area of fluffgrass averaged 0.19 percent cover on the former and 0.51 percent on the latter; and on only one sample was it as great on the protected side as it was on the grazed side. On the other hand, in areas dominated by creosotebush, protection appears to favor the development of fluffgrass. On an area of this sort within the fenced limits of Hot Springs, basal area of fluffgrass—the only grass present—averaged 1.26 percent cover; whereas on a similar area immediately outside, it averaged 0.13 percent. Similar instances were observed throughout the study area. Fluffgrass appears to be the least exacting of the grasses in its habitat requirements; it was found in dry upland sites and in most washes, where it occupied islands and bars and even a few channels that had not been active for a year or more.

BURRO GRASS

Scleropogon brevifolius is typically found on heavy soil in swales, although it was observed growing vigorously and in considerable abundance among creosotebushes on very sandy upland. It accounted for more of the grass cover of the area as a whole than any other species (Table 1). Burro grass was measured on 27.0 percent of the samples and was recorded on an additional 6.3 percent. Creosotebush was recorded on 91 percent of the burro grass samples, which did not differ significantly from the expected value. On the other hand, tarbush fell on 76 percent of the burro grass samples within its range, exceeding the expected value by a highly significant amount; and mesquite was found on 22 percent, which was very significantly less than the expected. Association with Mexican tea was likewise very significantly less than the expected, and that with *Opuntia leptocaulis* significantly more (Table 4). The other minor shrubs and all the grasses except tobosa grass (*Hilaria mutica*) were associated with burro grass approximately to the degree expected on the hypothesis of random assortment.

Campbell (1931), in his studies of succession on clay soils, found that burro grass was the first grass to invade such soils, where its stoloniferous habit allowed it to increase rapidly when grazing pressure was not excessive. He found that it persisted in greater or less amounts into the final stage, where tobosa grass became dominant on clay soils, and a mixture of these and other grasses with tarbush occupied gravelly clays. These findings are consonant with the present one that burro grass is associated with tarbush and tobosa grass more often than could be expected on the hypothesis of random assortment, and with mesquite and Mexican tea less often. On the other hand, in the present studies, results from 100-foot-line samples taken across the fence between lightly and heavily grazed areas of burro grass revealed no harmful effect of grazing.

BUSH MUHLY

Muhlenbergia porteri, a highly palatable grass, was usually observed growing in the protection of shrubs. In areas from which livestock had been excluded for a number of years, however, it was found in the absence of such protection, either associated with other grasses or as the only grass growing in the interstices among creosotebushes. Although it was common in the study area, it was never abundant on any site.

Bush muhly was measured on 11.8 percent and recorded on another 21.0 percent of the sampling sites. Percentages of these samples upon which it was found with creosotebush, tarbush, and mesquite were approximately those expected on the hypothesis of random assortment. With Mexican tea, *Optunia macrocentra,* and *Rhus microphylla*, association exceeded the expected by highly significant amounts; and the same was true of that with fluffgrass. The observed over-association with Mexican tea and Rhus suggest that bush muhly is favored by sandy soil.

BLACK GRAMA

Bouteloua eriopoda was probably the "winter grama" of which Emory wrote (1848). In the area of study, it is regarded as the most valuable forage species; and, where it has not been grazed out and replaced by half-shrubs or shrubs, it is usually dominant on upland areas. The soil on which the species is found at its best is usually sandy but rather firm; it was rarely if ever observed in good stands on shifting soil, probably owing to its propagating by stolens, for which a shifting substrate makes rooting difficult. Plants are found also on gravelly or stony soil, in which the soil matrix may be loamy.

Black grama was measured on 18.1 percent of the samples and recorded on an additional 8.4 percent. Creosotebush was recorded with it on 78 percent of these samples; this and the association with *Opuntia leptocaulis* were significantly less than the expected. Association with tarbush, mesquite, and most of the minor shrubs was approximately as expected; whereas that with Mormon tea and fluffgrass exceeded the expected by highly significant amounts, and that with bush muhly by a significant amount. This pattern of association accords with the field observation, mentioned above, that black grama is most often found on sandy soil.

Several authors (Jardine & Hurtt 1917; Jardine & Forsling 1922; Nelson 1934; Wooton 1915, 1922) have emphasized the harmful effects of over-stocking black grama ranges and the benefits of moderate grazing or of periods of complete protection. The point is reemphasized by data from the previously mentioned 12 samples taken above Hot Springs. After 8 years of protection or occasional light grazing, total basal area of grasses was 2.60 percent cover in the protected right-of-way and 1.11 percent on the range. Basal area of black grama averaged 2.01 percent cover on the former and 0.43 percent on the latter. Only scattered shrubs were present in these

lobes of grassland, but a few small creosotebushes were coming in, particularly at the edges.

OTHER GRASSES

Bouteloua curtipendula, side-oats grama, was most often observed in situations with above-average moisture conditions—near the upper edge of the shrub belt, on north-facing slopes, in depressions, and in washes. It was measured on 5.9 percent of the samples and recorded on an additional 4.4 percent. Association with most shrubs was approximately that expected from random assortment. With Mexican tea and *Rhus microphylla*, however, it exceeded the expected by significant and highly significant amounts, respectively (Table 4). Association with bush muhly, fluffgrass, and black grama was greater than the expected by highly significant amounts. This pattern of association would suggest that the species appeared most often on areas of sandy soil.

Aristida fendleriana, Fendler three-awn, was measured on but 8.3 percent of the samples; but, on the area as a whole, it accounted for 26 percent of the basal area due to "other grasses" (Table 1). It was recorded on an additional 2.0 percent of the samples. Association with black grama and with side-oats grama exceeded the expected by highly significant amounts; that with the shrub species was approximately as expected.

Sporobolus cryptandrus, sand dropseed, although it was observed throughout the area, was recorded on the samples mostly in the northern half. It was measured on 7.8 percent and recorded on an additional 2.0 percent of the sampling sites. Its association with creosotebush—70 percent—was significantly less than the expected; that with black grama and Fendler three-awn exceeded the expected by highly significant amounts. Association percentages with other species did not differ significantly from the expected values.

Hilaria mutica, tobosa grass, was observed as far north as 28 miles south of Socorro. It is typically a grass of heavy soils in swales, where it receives extra moisture in the form of runoff from the adjacent upland. It was, however, observed also on the sides and tops of dry hills. Although its presence in such situations is regarded by some practical range men as indicative of past over-stocking, the writer is not satisfied that this is true. The underlying factors that permit a swale grass such as tobosa to grow in these apparently dry sites need investigation.

Tobosa grass was measured on 7.3 percent and recorded on an additional 4.5 percent of the total number of samples. Of the samples within its range, however, it was measured on 11.0 percent and recorded on another 5.0 percent. Association with the various species of shrubs and grasses, except fluffgrass and burro grass, was approximately the expected on the hypothesis of random assortment. With the two grasses mentioned, it was greater than the expected by highly significant amounts (Table 4). The degree of association withe burro grass supports the general field observation that tobosa grass is found more often on the heavier soil phases.

Hilaria jamesii, galleta grass, was found in approximately the northern one-third of the area. Its observed range overlapped that of tobosa grass by about 20 miles. The two were never recorded on the same sample, but the habitat differences, if they exist in the area of overlap, were not investigated. Within this range, a few specimens were collected that had the glumes of one species and the hairiness and general aspect of the other, suggesting that the two may hybridize to some extent. The relations of the two species in the overlapping area would appear to offer an interesting problem of a minor sort.

Galleta grass was measured on 7.8 percent of the total number of samples and was recorded on another 2.0 percent. Within its observed range, however, analogous percentages were 23.5 and 6.9. Black grama appeared on 55 percent of the galleta grass samples, which was very significantly greater than the expected value. Association with Fendler three-awn was significantly greater than the expected, while that with the shrubs and the other grass species was approximately as expected from random assortment.

Aside from the inferences drawn from the observed degrees of association of the various species and already mentioned in the discussion of the individual species, one or two others may be pointed out. The fact that black grama was associated less often with creosotebush and more often with six of the eight other grasses tested than could be expected from random assortment, would seem to imply that even those grasses that appear to be associated at random with creosotebush tend to occupy the less unfavorable habitats. That this is true even of fluffgrass, which, as was mentioned above, appears to be the least exacting of the grasses in its habitat requirements, is suggested by its significant positive association with such inhabitants of sandy soils as Mormon tea, *Rhus microphylla*, and black grama on the one hand and with tobosa grass on the other. The same reasoning may be applied to other pairs of grasses that are apparently randomly associated with the major shrubs.

Half-Shrubs

Suffrutescent and suffruticose plants have been considered as a separate group because they contribute to the year-long cover as the shrubs do, and yet they are often found growing under the shrubs. Thus, to group them with the shrubs would create a false impression of the percentage of the surface actually covered. The same criticism might be advanced for inclusion of some of the smaller shrubs in that group, *e.g., Krameria parvifolia, Parthenium incanum,* and some of the cacti; but the amount of over-lap seems to be greater in the case of those species included here as half-shrubs.

As a group, the half-shrubs were measured on 39.2 percent of the samples and were recorded on another 15.7 percent. Association of the group with each of the three major shrub species, both as

to total number of samples and as to the samples upon which one of these species accounted for half or more of the shrub cover, was approximately as expected with random assortment; and the same is true of that with the grasses as a group.

Gutierrezia sarothrae, snakeweed, was the only one of the group to be measured on 10 percent or more of the samples. It was measured on 27.9 percent of them and recorded on another 14.7 percent. Association with the three major shrub species was approximately that expected on the hypothesis of random assortment. That with mariola was very significantly less than the expected; with Mexican tea, Mormon tea, and *Rhus microphylla,* association exceeded the expected values by highly significant amounts, and the same was true with black grama, tobosa grass, and fluffgrass. With galleta grass, it was significantly greater than the expected (Table 4). This pattern of significant association with these three shrubs and the grasses and lack of association with mariola suggests that the moisture requirements of snakeweed may be somewhat higher than those of other shrubs and half-shrubs; this is consonant with the fact that it cannot withstand competition in good stands of grasses.

In 1915, Wooton wrote that snakeweed was so infrequent on range that was not overstocked that it escaped notice and had often been sent to him as a recently introduced weed. He pointed out that the grama grasses, if given the chance, would crowd it out; and this is a common observation today. Data from the 12 previously mentioned samples above Hot Springs serve to illustrate the point quantitatively. On the protected right-of-way, cover due to snakeweed was 0.41 percent; that on the heavily grazed range, 1.04 percent. Moreover, dead snakeweed plants were common on the protected side and rare or lacking on the range.

Dyssodia acerosa was the only other half shrub to appear on 10 percent or more of the samples. It was measured on 7.8 percent and recorded on an additional 3.0 percent of them. With all of the tested species except fluffgrass, association was approximately that expected on the hypothesis of random assortment. With fluffgrass it was significantly greater than the expected, chi-square exceeding the 2 percent level of probability. While these two species increase with overgrazing of grassland, they seem to increase also when shrub areas are protected, as has been mentioned above for fluffgrass and will be discussed for the other species in a later section. This may account for the observed degree of association of the two.

FORBS

During the period of sampling, forbs were never abundant in the area, probably owing to below-average rainfall. The fact that the samples were taken from early spring to late fall serves further to make the data less representative for so large an area than they might have been had a small area been sampled during these seasons. The summer of 1950 was relatively wet, and forbs were abundant in the vicinity of Las Cruces, particularly in sandy areas.

As a group, forbs were measured on 27.9 percent of the samples and were recorded on another 21.1 percent. Association of the group with the three major shrubs species, both with respect to the total number of samples upon which they occurred and to the number upon which one of the three accounted for half or more of the shrub cover, was approximately equal to that expected on the hypothesis of random assortment. On the other hand, association with the grasses as a group and with the half-shrubs as a group exceeded the expected values by highly significant amounts. None of the 58 species recorded on the samples was measured on 10 percent of the samples, and only two were recorded on that many or more.

Euphorbia albomarginata was measured on 8.8 percent of the samples and was recorded on another 2.5 percent. Although the impression one gets from field observation is that it requires a little more water than is to be found under average conditions, since it is to be found in most washes, it was observed occasionally among creosotebushes where there was a well developed erosion pavement; and its association with the three major shrub species was approximately that expected from random assortment. Association with black grama and with Fendler three-awn was significantly greater, and that with snakeweed and with galleta grass very significantly greater, than the expected values. This might be interpreted as supporting the impression of greater moisture needs.

Perezia nana, desert holly, was measured on 6.9 percent and recorded on an additional 13.7 percent of the sampling sites. It was associated with creosotebush and bush muhly significantly more often than could be expected by chance. The excess of association with *Opuntia macrocentra,* tarbush, and black grama was highly significant. Although a cursory examination of the area and the observed degree of association with creosotebush might give the impression that desert holly is a denizen of shallow soils, its degree of association with the others mentioned implies that this is not true, and it is concluded that, although its presence probably indicates deterioration of the site, even with creosotebush it is more often found on the less unfavorable sites.

VEGETATION OF WASHES

Wooton (1915) considered the plants found in washes to be species of the bordering foothills that have followed down the drainage channel or those that have worked back up from the valley into which the channels spill, plus a few that have come in from the adjacent upland. He attributed this distribution to local conditions of water and air drainage. In the present studies, of 31 species of trees and shrubs, 4 species of half-shrubs, 22 of grasses, and 22 of forbs that were recorded in 93 washes, 23 shrubs and all of the half-shrubs, grasses, and forbs were

observed on the upland. Several of the most common shrubs and forbs and a few of the grasses, however, were found only on deep sand, in swales, or in borrow pits. Of the eight species of trees and shrubs not observed on the upland, *Acer negundo* var. *interius, Juglans rupestris* var. *major,* and *Platanus racemosa* var. *wrightii* were observed only in one or more of the broad, deep valleys of Alamosa, Cuchillo, Palomas, and Las Animas arroyos; and the other five species were very infrequent also. Owing to the presence of many of the commonest wash species on deep sand, in swales, or in borrow pits along highways, the writer believes that, with the possible exception of the trees mentioned, the factor of soil moisture far outweighs that of air drainage in determining the nature of the vegetation in washes.

Lists of species were made in 93 washes at the points at which they crossed U. S. highway 85 or at other convenient places. The species listed were those growing on islands, in the channels, and along the edges of the channels. Not all of these washes were examined for plants other than shrubs; consequently, in the present analysis only the shrubs will be considered. Nine shrub species were common, and 22 other trees and shrubs were recorded. Of the nine commonest, mesquite was recorded in the largest number of washes—a total of 54. It was the most abundant shrub in 13. Corresponding data for the other eight follow: *Hymenoclea monogyra* in 45 washes, most abundant in 17; apache plume (*Fallugia paradoxa*), 44 and 28; *Rhus microphylla,* 40 and 4; chamisa, 38 and 5; creosotebush, 36 and 1; *Brickellia laciniata,* 33 and 11; desert willow (*Chilopsis linearis*), 12 and 5; and tarbush, 12 and 2. The species most often found invading the channels and forming islands in these and other observations were desert willow, apache plume, *Hymenoclea monogyra, Brickellia laciniata,* and *Rhus microphylla.*

As was mentioned earlier, the watercourses of the study area are intermittent or ephemeral. Many of them may flow from one to several times during the summer and fall and then remain dry during one or more years. The water may run in a single, wide, relatively straight channel, which is often more or less deeply intrenched; or it may flow through a series of anastomosing channels, which may or may not be intrenched (Fig. 8). A common, but by no means the universal, condition is a single channel in the upper and a series of channels in the lower reaches; but either condition may prevail throughout the greater portion of the wash. The islands among the anastomosing channels usually support a cover of shrubs, or of shrubs, half-shrubs, and grasses. Indeed, it seems probable that many of these islands are formed as a result of a shrub's becoming established in the channel and acting as a barrier below which sediment may be dropped and other shrubs become established. The underlying factors that allow shrubs to become established in an apparently unobstructed channel are not clear; but numerous examples of small shrubs in such situations have been observed, and the process of island formation has been traced from single shrubs up to islands of considerable size. In the case of some species that become established in the channel, *e.g.,* desert willow and apache plume, the process is hastened by the shrub's being knocked down by a high flow and partially covered with sediment, after which a miniature thicket may spring up from the buried or partially buried branches. Not all of the islands are formed in this manner; some result from high flows that cut new channels around existing vegetation.

Fig. 8. An arroyo in which there is a network of channels. The shrubs are mainly *Brickellia laciniata, Chillopsis linearis, Rhus microphylla,* and *Prosopis juliflora.*

In such instances, however, the type of vegetation is usually different; it is usually creosotebush or mesquite, and often a mixture of the two.

The importance of islands formed from shrubs in the channel lies in the fact that washes in which they are abundant appear less likely to discharge damaging flows from their mouths than are those with long reaches of unobstructed channel. The stream appears to be broken up and slowed down to the extent that ordinary flows may be partially or wholly absorbed by the channels. Thus, during a period of five years of observation, two such arroyos on the College Ranch have never been observed to discharge water in streams larger than trickles onto the valley floor, although water has flowed in their upper and middle reaches; whereas arroyos with relatively unobstructed channels on both sides of these two have discharged considerable amounts of water during the same storm. Evidence of erosion in the two arroyos indicates that in the past they have carried large amounts of water at their mouths; and the writer is told that farming of the valley land immediately below one of them was considered too hazardous to be practicable. Now, however, crops are being grown on the land at comparatively small risk. Of course, during exceptionally heavy storms, these arroyos may be expected to spill water on the valley floor; but in the long run the likelihood of damage appears to have been lessened.

Establishment of shrubs in open channels may be dependent on, or at least facilitated by, the characteristic, noted above, of there being years during which the water does not run. Thus the seed might germinate in the moist bed immediately after a flow, and, given a year or more before the next flow, the

plant might become well enough established to withstand subsequent flows. The seeming lack of moisture that this condition might imply would hardly be a limiting factor in the continued growth of the plant, for moisture is present at shallow depths (6-8 inches) in washbeds, even after several months without rain. That small desert willow plants can withstand considerable abuse is demonstrated by the response of small transplants of this species. In the early spring of 1949, approximately 500 plants, ranging from three-eights to three-quarters of an inch in diameter at the butt, were set out in the bed of a wash 10 miles south of Las Cruces. They were planted in holes two to three feet deep and approximately six feet apart each way and reaching from bank to bank of the channel, which was only slightly intrenched. Immediately after planting, the whips were cut back to heights approximating five inches. The exposed parts were less than a half-inch in diameter. Survival in the late spring, before the wash ran, was nearly 95 percent; that in the spring of 1950, after three low to moderate flows during the preceding summer and fall, was 56 percent. Several moderate to moderately heavy flows occurred during the summer and fall of 1950, and survival in the following December was 40 percent. There appeared to be no pattern of survival, either with regard to size of plant or to position in the channel. The response of 1000 plants set in the edge of the large and active Rincon Arroyo, 30 miles north of Las Cruces, was in sharp contrast to this. Survival after planting was practically complete, but the flows of the first season completely wiped out the planting.

RESPONSE OF VEGETATION TO PROTECTION

On Upland

If it is a valid hypothesis that the area in question is desert grassland and its present domination by shrubs represents a grazing disclimax or successional stages, protection from grazing should effect changes in the vegetation. Once grass has been completely lost from an area of desert grassland, however, even without loss of soil or invasion of shrubs, the return of a comparable grass cover is a long, slow process (Gardner 1950). Where shrubs are in control and soil loss has been as great as is indicated by observations such as are illustrated in Figure 2 and by the more exhaustive data of Cooperrider and Hendricks (1937), the process could be expected to be much slower.

Wooten (1915) attributed the distribution of shrubs —particularly that of creosotebush—on the mesas to soil aeration or, possibly, to the amount of available water in the porous, gravelly soils. He said, however, "it is not uncommon to find in these brush-covered areas spots of [finer surface soil], from a few feet to several acres in extent, upon which occurs an almost pure stand of grass." He attributed the presence of these spots to local deposition of wind-blown material. On the basis of records of early travelers describing abundant grass on areas now occupied by shrubs and of the present observations indicating soil loss, it seems likely that many of the spots represented relicts of a more widespread and more nearly general condition. Apparently supporting this assumption is the fact that during the present studies no such spots "of several acres in extent" were observed. If the assumption is true, profound soil changes may be necessary for a return to grass, and the time required may be very long. There are a few indications, however, that the soil is not entirely limiting; and, given protection and other favorable conditions, such as a series of moist years and a source of seed, grasses might become established in some areas under existing soil conditions.

Data of Booth (1941) and of Costello (1944) indicate that return of a perennial grass cover to abandoned farm land followed a sigmoid curve when cover was plotted against time. Booth's results showed that, in the true prairie of Kansas and the prairie-forest transition of Oklahoma, 31 years were insufficient to bring back the original prairie cover; and Costello estimated that 25 to 50 years were necessary for a return to the mixed prairie association in eastern Colorado. Assuming a similarly shaped curve for return of grasses to the creosotebush and other shrub-covered sites of the study area, the time required may be expected to be several times as long as those indicated by these data. Owing to the low rainfall, the loss of soil, the scarcity of propagules, the presence of shrubs, and other factors, the time consumed by the lower, gently sloping part of the recovery curve may be expected to be longer than the entire time for recovery in the more favorable environments of the authors mentioned. Among the other retarding factors is pressure of rodents and rabbits (Norris 1950).

The assumption that the initial stages of recovery are of long duration is supported by data collected from an area on the College Ranch, which lies 10 miles north of Las Cruces on the east side of the Rio Grande, and an adjacent one just south of it. Grazing on this part of the ranch had been from very light to none for a period of 20 years previous to the sampling; that on the outside area was uncontrolled. Seven samples were taken at half-mile intervals in each area along a trail road running approximately north and south. The samples comprised the usual two 100-foot lines and supplemental list of species. Creosotebush dominated both areas (Table 5). No grasses except a very few isolated clumps in washes were observed in the outside area; on the ranch area, basal area of grasses was very low, averaging 0.03 percent cover, most of which was fluffgrass. Total shrub cover, as well as that due to creosotebush, was somewhat higher inside than out, but both were comparable on the two areas. No forbs were measured in either area; but two species were recorded on the samples outside and seven on those inside. Crown spread of half-shrubs averaged

0.1 percent cover outside and 0.7 percent inside. This difference in half-shrubs appears to be of considerable importance from the point of view of recovery. One of the first visible changes under protection is an increase in this class of plants. The fence between the two areas in question was followed for a distance of approximately two and a half miles for the purpose of observing differences in half-shrubs on the two sides. No quantitative data were taken, but it was observed that these plants were more numerous inside than out, especially in the shallow water runlets. In a few of these very small gullies, the plants were growing right up to the fence without extending across it. The effective factors that bring about an increase of such unpalatable plants as snakeweed, *Dyssodia acerosa,* and *Zinnia pumila* under protection from grazing are far from clear, but the phenomenon was observed in other areas. Throughout the study area, places that have been protected by accident or by design tell the same story of slow recovery, although it is somewhat more rapid on sites where a little grass remained at the time protection was begun. It is, of course, more rapid also on north-facing slopes and in places where water concentrates.

Table 5. Vegetation on contiguous areas upon which grazing was light on one and uncontrolled on the other. Seven samples on each at 0.5-mile intervals.

Species	Grazing uncontrolled	Grazing light
Grasses (basal area, percent cover)		
Bouteloua eriopoda	No grasses	Trace
Tridens pulchellus	seen	0.02
Total		0.03
Shrubs (crown spread, percent cover)		
Ephedra trifurca	0	.1
Flourensia cernua	0	1.1
Fouquieria splendens	Trace	.4
Larrea divaricata	17.7	18.6
Mammillaria macromeris	0	.2
Parthenium incanum	.5	.3
Prosopis juliflora	0	.3
Yucca baccata	0	.1
Total	18.2	21.0
Half-Shrubs (crown spread, percent cover)		
Dyssodia acerosa	0	.1
Gutierrezia lucida	.1	Trace
Zinnia pumila	Trace	.6
Total	.1	.7
Forbs	None measured 2 spp. observed	None measured 7 spp. observed

The difference in rate of recovery on areas devoid of grass at the time protection was begun and on those upon which there was a residuum of grass cover present is illustrated by a comparison of data collected north of Hot Springs, part of which have been referred to in the discussion of grasses. The assumption is made that, since split samples were used, with the highway fence as the dividing line between the two halves, conditions were similar on the two portions at the time of fencing; and that, where the gramas and other climax grasses are now present on the grazed side, they were originally present equally on both sides, whereas they were absent from both sides on the areas where they do not now appear on the protected side. The data were taken in interdigitating lobes of the two types of vegetation. On the samples upon which it is assumed there was a residuum of grasses, shrub cover amounted to 1.5 percent in the protected and to 2.5 percent in the grazed area; basal area of grasses, to 2.60 percent and 1.11 percent, respectively, of which fluffgrass made up 7 percent and 46 percent. On the samples for which the opposite assumption is made, shrubs averaged 8.9 percent cover on the protected side and 7.4 percent on the grazed portion; basal area of grasses, 0.31 percent and 0.44 percent, of which fluffgrass accounted for 100 percent and 70 percent, respectively. The remaining 30 percent of the grass cover on the grazed area was due to burro grass, which probably means that the assumption of similarity and of no residuum at the time of fencing was not quite valid; nevertheless, the data illustrate adequately the difference in recovery rates.

In Washes

It has long been recognized that removal of vegetation by heavy grazing increases surface runoff. Thus Gilbert (1879) attributed a part of the rise in the level of Salt Lake to the increase of runoff caused by destruction of vegetation by grazing of livestock on the contributing drainage areas; and Wooton (1908) and Rich (1911) ascribed the gutting of valleys by erosion in the Southwest to the same cause. In the intervening years sinces these authors wrote, so much corroborating evidence has accumulated that the conclusion is accepted as almost axiomatic.

Throughout the study area, changes in vegetation were noted in gullies and arroyos in protected or lightly grazed areas. Grasses and other herbaceous vegetation were observed to be coming into small and large gullies, and shrubs and grasses to be increasing in arroyo beds. Thus in a large area to the east of the river above Socorro, sacaton (*Sporobolus wrightii*) was found invading a gully that had formed along an old highway; and side-oats grama was found in appreciable amounts in smaller gullies. At the time the observations were made, the area had been protected from grazing for approximately 10 years.

In the southern part of the study area, data were collected in arroyos in the areas that were sampled for upland vegetation on and adjacent to the College Ranch (Table 6). The channels in all four of these washes were of the type that repeatedly break up and reunite. Samples consisting of two 100-foot lines were taken at half-mile intervals from the mouth of each wash. Although the data indicate that basal area of grasses in the washes on the ranch was low, grasses were common throughout the

entire length. Only a trace of grass was measured in the one outside; and this truly represents the condition of the washes in the unprotected area. Several others were carefully examined by walking through their entire lengths, and grass clumps were found only rarely in them. On the ranch, grass was observed in the small tributaries; but this was not true of those on the outside area. While the grass in these tributaries probably retards the water on its way to the main arroyo, allowing part of it to be absorbed, it is hardly credible that the small amounts measured in the main washes could exert much influence on the flow of water. A more probable hypothesis seems to be that the presence of grasses there is a reflection of ameliorated conditions brought about by protection of the contributing drainage area and the increase of shrubs in the wash. Cover of half-shrubs and of forbs in the washes was no different under the two degrees of grazing. Shrub cover in the washes of the lightly grazed area, although somewhat higher than that in the wash in the heavily grazed area, was not greatly so. Composition, however was markedly different: creosotebush made up 57 percent of the shrub cover in the heavily grazed wash, but only about 16 percent of that in the lightly grazed ones. In the other heavily grazed washes examined, the percentage of creosotebush may not have been so high as in the one measured, but it was still noticeably higher than it was in the lightly grazed washes; and this was true of the corresponding reaches of one that extended from the college area into the heavily grazed one. In this wash, too, grasses were common in the protected reaches and rare in the uncontrolled section. In the sampled washes, desert willow, apache plume, *Rhus microphylla*, and *Brickellia laciniata* made up well over half of the shrub cover of those on the College Ranch, whereas the first three of these species were lacking from the samples of the heavily grazed wash. Scattered representatives, however, were observed, and they made up more of the cover in the similarly grazed washes examined. *Brickellia laciniata* accounted for approximately the same percentage of the shrub cover in all four washes. Although these four shrubs occupied islands under both conditions of grazing, this condition appeared to be more marked where the grazing was light, and it appears that formation of such islands as described above is favored by some degree of protection. How much of the apparent reduction in flow can be attributed to the presence of these islands, and how much to changes brought about by protection of the contributing drainage basin, the writer is not as yet prepared to say; nor is he prepared to evaluate the role of the latter factor in bringing about conditions that facilitate the observed changes in wash vegetation and the formation of the islands—that is, whether the changes in shrub cover, like those of the grasses, merely reflect better conditions on the drainage area brought about by protection. It seems safe to assume, however, that both of the factors—presence of islands of vegetation in the washes and protection of the contributing area—contribute to the end result—reduction of arroyo flow—and that some degree of protection is the starting point.

TABLE 6. Vegetation in washes in areas where grazing was light or where it was uncontrolled. Samples taken in wash at 0.5-mile intervals from mouth.

	Uncontrolled grazing	Light grazing	Light grazing	Light grazing
GRASSES (basal area, percent cover)				
Total	Trace	0.08	0.03	0.06
SHRUBS (crown spread, percent cover)				
Acacia constricta	1.7	0	0	0
Atriplex canescens	0	2.5	.6	1.4
Brickellia laciniata	3.2	3.7	4.6	3.2
Chilopsis linearis	0	.9	2.4	1.6
Fallugia paradoxa	0	.7	5.8	4.4
Larrea divaricata	7.9	2.3	3.2	3.1
Prosopis juliflora	0	2.0	2.0	4.0
Rhus microphylla	0	2.2	0	.8
All others	1.0	.8	.7	.8
Total shrubs	13.8	15.1	19.3	19.3
HALF-SHRUBS (crown spread, percent cover)				
Total	2.0	2.6	.7	1.4
FORBS (number of plants per 100-foot line)				
Total	0.25	.50	.37	.66

SUMMARY

Between 1946 and 1949, studies were made of the vegetation of the uplands and the washes of the Rio Grande valley between Las Cruces, New Mexico, and the mouth of the Rio Puerco. The northern limit of the studies is approximately that at which *Larrea divaricata* ceases to be a prominent component of the vegetation. Testimony of travelers and military expeditions of the 19th century and of long-time residents of the valley points to the conclusion that the area was once grass-covered except in certain limited areas. Shrubs were, however, probably scattered among the grasses in many places. In an area where annual evaporation is several times the precipitation, which in the valley ranges from 8.5 to 12 inches, grazing that in more favorable habitats would not be excessive penalizes the grasses and favors unpalatable shrubs and half-shrubs. Such has unquestionably been the case in this valley.

The present vegetation of much of the area is dominated by shrubs, and grass cover is sparse or wanting over wide stretches. Shrubs are now in possession of sites upon which black grama grass hay was cut and baled within the memory of living residents. In the shrub belt, crown spread of shrubs averaged 14.0 percent cover, of which 63 percent was due to *Larrea divaricata*, 9 percent to *Flourensia cernua*, and 15 percent to *Prosopis juliflora*. The remaining

13 percent of the shrub cover was made up of 32 species. As indicated by degree of association with other species and by field observations, *Larrea divaricata* is invading other plant communities. This process seems to be preceded or accompanied by a loss of surface soil, as is indicated by the presence of old shrubs of this species or of *Flourensia cernua* that appear to have short trunks four to eight inches in height where the soil has been washed or blown away exposing the taproots. Further evidence is the development of an erosion pavement as the creosotebush becomes dominant. Of the 204 sampling sites upon which the general data are based, creosotebush was dominant on 65 percent, tarbush on 7 percent, and mesquite on 7 percent. Tarbush was found only in approximately the southern two-thirds of the area, and within this range it was dominant on slightly more than 9 percent of the sampling sites. Creosotebush was observed on 86 percent of the samples, mesquite on 35 percent, and tarbush, within its geographic range, on 50 percent. On 2.5 percent of the samples, creosotebush was the only plant observed. It was the only species to appear alone on the samples.

Of the perennial grasses, 21 species were recorded on the sampling sites. Only four of these, however, were measured on 10 percent or more of the samples. Of these four, *Tridens pulchellus* was recorded on 39 percent of the samples, *Scleropogon brevifolius* on 33 percent, *Muhlenbergia porteri* on 33 percent, and *Bouteloua eriopoda* on 26 percent. *Scleropogon brevifolius* contributed more to the plant cover than any other grass. Basal area of grasses averaged 0.36 percent cover. Measurements in protected grassland in the area gave values approximating 10 times this amount.

Ten species of half-shrubs were recorded. Of these, only *Gutierrezia sarothrae* was measured on 10 percent or more of the samples. It appeared on 43 percent of them. During the period of sampling, forbs were not abundant; although 44 species were recorded on the samples, no species was measured on as many as 10 percent of them.

Analysis of the degrees of association between species indicated that half-shrubs, forbs, and grasses tend to occur on the less unfavorable sites, and this is true also of tarbush and certain of the minor shrub species.

Protection of areas that have a residuum of the grasses brings about a moderately rapid recovery of the grasses. Where such a residuum is absent at the time protection is begun, increase of grass cover is extremely slow. One of the first visible effects of protection on the latter sort of area is an increase of half-shrubs in the small gullies and of these and grasses in the small tributaries of the washes. In the wash channels, such shrubs as *Chilopsis linearis, Fallugia paradoxa,* and others increase and form islands of vegetation that tend to break up and slow down the flow, allowing greater or less amounts of the water to be absorbed. In one area, it appears that 20 years of protection, while having had little measurable effect on the upland vegetation, has reduced the runoff leaving the area.

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